

# **Did Neanderthals and Carnivores Compete for Animal Nutritional Resources in the Surroundings of the Cave of Zafarraya?**

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This paper proposes a novel approach to study the interactions of Neanderthals and carnivores in the cave of Zafarraya by comparing the lithic archaeological and faunal records with a statistical path analysis, taking into consideration the ecology of the main carnivore predators and large herbivore prey foraging in the surroundings of the cave. The results of the analyses confirm and shed further light on previous taphonomic and zooarcheological research. The findings concur with the two-species Lotka-Volterra competition model for resources which stipulates that when niche overlap is complete the species with the larger fitness excludes the other. Our analysis shows that in the immediate vicinity of the cave, the fitness of *Panthera* was greater than Neanderthals', i.e. when *Panthera* was present it

excluded Neanderthals as evidenced by the record of *Capra* and *Rupicapra* remains. It also shows that further in the southern hills and the polje where large herbivores roamed, Neanderthals had a greater fitness than carnivores which translated into their primary accumulation in the cave of remains of *Cervus elaphus* and other large herbivores. Coexistence from occasional niche overlap is apparent when one or the other predator scavenged, but from a time prospective it must have been short periods linked to seasonality, weather conditions and occupation randomness. In Zafarraya, the archaeological record would indicate that the degree of fitness of the herbivore prey accumulators, carnivores or Neanderthals, was related to the nature of the geomorphological domains in the vicinity of the cave and the favored foraging areas of hunted herbivores.

**Keywords:** ZAFARRAYA, NEANDERTHALS, CARNIVORES, INTERACTIONS, HERBIVORES, *CAPRA PYRENAICA*, LITHICS, PATH ANALYSIS

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## Introduction

Interactions between Neanderthals and carnivores have been the object of diverse interpretations ranging from: Neanderthals regularly scavenged the carcasses procured by carnivores (Stiner, 1994) or Neanderthals had primary access to prey (Marean, 1998), to mixed Neanderthal procurement strategy resulting in regular hunting and occasional scavenging depending on varying circumstances affecting foraging (Stiner, 1991). These diverse faunal exploitation models to explain Neanderthal subsistence strategies rely on generally accepted zooarcheological methodologies, namely skeletal element abundance, surface modifications and mortality profiles. However, various authors (Marean & Assefa, 1999; Domínguez-Rodrigo & Pickering, 2003) warn that caution must be exercised in interpretative scenarios based solely on zooarcheological methods such as for example resolving the question of human bone transport by relying on differential bone element representation or drawing inference about primary or secondary access to carcasses from surface modifications resulting from multiple superimposed processes. A broader spectrum of methodologies to understand the

variability in Neanderthal faunal exploitation and subsistence strategies is outlined in Burke (2004) covering topics such as carbon and nitrogen stable studies, impact of environmental changes, carnivore extinction patterns and lithic procurement sources. In the present paper we will use a novel approach to shed some further light on the interactions of Neanderthals and carnivores in the cave of Zafarraya, by comparing the lithic archaeological record of the site with the faunal record and taking into consideration the ecology of the main carnivore predators and large herbivore prey foraging in the surroundings of the cave.

The authors of detailed taphonomic and zooarcheological analyses of the cave of Zafarraya faunal assemblage (Barroso & Lumley, 2006) propose a faunal exploitation model showing that Neanderthals who occupied the cave were specialized hunters of *Capra pyrenaica*, the most abundant species unearthed. However, Neanderthals of Zafarraya inhabited an environment rich in herbivore prey diversity with regard to food availability, and taking into account the joint presence and continuous occupation of carnivore species in the site, one could argue that this nutritional exploitation model does

not reflect fully the interaction between carnivore predators and Neanderthals in the cave, and thus might be incomplete. The question of Neanderthal and carnivore occupation overlap in the cave, and whether these two sets of occupiers occasionally competed for the nutritional resources available in its surroundings is therefore relevant, and represent an interesting area of research (Burke, 2000; Bar-Yosef, 2004; Patou-Mathis, 2000) which will be addressed in the present study.

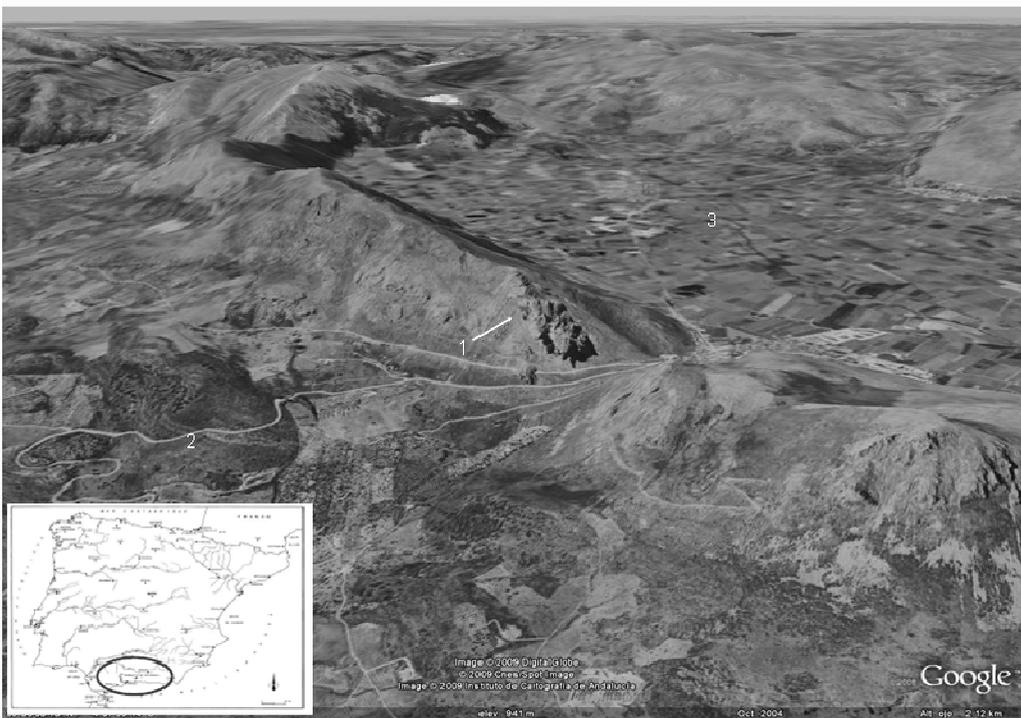
We can envisage three possible scenarios with regard to Neanderthal- carnivore coexistence in the cave of Zafarraya: 1) Neanderthals dominate carnivores and exclude them from the proximate ecological system, or vice versa; 2) Neanderthals niche overlap with carnivores is complete, and due to larger fitness, Neanderthals exclude carnivores, or vice versa; or 3) Neanderthals niche overlap with carnivores is complete, but Neanderthals are not able to exclude them from the nearby ecological environment: they coexist together. To ascertain which of these three scenarios is the most probable we will focus our analysis on two issues: first, with regard to Neanderthal / carnivore occupation overlap in the cave, how did these two sets of predators interact for the nutritional resources of herbivore elements and, second, how did they compete with regard to *C. pyrenaica*.

Drawing on the taphonomical and zooarcheological analyses of Zafarraya (Barroso & Lumley, 2006) we will apply a path analysis to the faunal data. Path analysis is a statistical approach (Olobatuyi, 2006) extensively used in the social and biological sciences which will contribute to a better understanding of the fauna procurement strategies of Neanderthals and carnivores in Zafarraya.

## Background of the cave of Zafarraya

Located in the Axarquía region in the province of Malaga, Spain, on the southern boundary of the province of Granada 25 km north of the Mediterranean shore, the cave of Zafarraya stands at an altitude of 1,022 m at the foot of the Sierra de Alhama and opens up towards the South at the top of a very steep escarpment (Figure 1). It was discovered in October 1979 by Cecilio Barroso (Barroso et al., 2003; Barroso & Lumley, 2006) and under his direction eight excavation campaigns took place from 1981 to 1983 and from 1990 to 1994. The unearthing in an archaeological context in 1982 and 1983 of a rich Neanderthal human fossil accumulation along with an abundant Mousterian lithic assemblage and rich faunal ensembles contributed to making the cave of Zafarraya a leading reference Neanderthal site in Europe. It provided the evidence of the late survival of Neanderthals in southern Iberia before their presumed disappearance (Jimenez-Espejo et al., 2007; Sørensen, 2011; Jennings et al., 2011; Bradtmöller et al., 2012; Schmidt et al., 2012).

The cave of Zafarraya is part of the karst of the Sierra de Alhama limestone range. This Sierra is cut by a transverse valley, the pass of the Boquete de Zafarraya, which connects the Zafarraya polje in the north to the highly ravined southern slopes of the hills leading towards the coast with a typical Mediterranean landscape. Towards the east are found the massive mountain peaks of Sierra de Tejada reaching an altitude of 2100 m. The polje, today a fertile well irrigated vast plain surrounded by Sierra Gorda, Alhama and Tejada, was formerly a lake which was emptied as the result of neotectonic uplift. The inhabitants



*Figure 1. Location of geomorphological domains surrounding the site: 1) Zafarraya cave, 2) southern sloping hills and 3) polje.*

of the cave of Zafarraya were living in an environment morphologically close to the present day one. The hydrology of the polje favored a grassy landscape which attracted herbivore herds migrating during dry summertime from the lower parts of the Mediterranean coast through the pass of the Boquete de Zafarraya.

Presently the cave is 23 m long, 0.5 to 3.5 m wide and 1 to 1.95 m high. It is divided into three parts (Barroso *et al.*, 2003:60): the entrance chamber (Sala de Entrada), the back chamber (Sala del Fondo) and the far-end diverticule which has not been excavated. Prior to excavations

in 1981 the site was cleared of disturbed deposits emanating from early 20<sup>th</sup> century clandestine excavations in the back room. A stratigraphic survey of the back chamber revealed a sequence of 6 m, with the upper 4 m showing archaeological material. The excavations of the site reached a depth of 1.40 m. Both the entrance and the back chambers were excavated and produced a very rich archaeological material of Neanderthal remains, lithic industry and faunal assemblages. Archaeostratigraphic units of the excavated sediments were defined according to lithic industry accumulation, and stone and bone

distributions. Based on field observations, the stratigraphy (Barroso & Lumley, 2006:153-411) has been divided into 3 complexes. The upper complex between -49 and -116 cm below 0 reference point, preserved mainly in the Sala de Entrada, is composed of blackish silty sand with small stones and contains essentially Neolithic and Upper Palaeolithic, mainly Solutrean, archaeological artifacts. The middle complex between -116 and -525 cm composed of brown ochre silty sand matrix with embedded broken stones contains the Neanderthal remains, the Mousterian industry and the faunal remains which will be the object of the present research. The lower complex, visible in the Sala del Fondo and the far-end diverticule is composed of archaeologically sterile beige to red clayish quaternary silts.

The study of the abundant materials discovered in the site has been presented in the publication of two extensive monographs covering the multidisciplinary aspects of this important archaeological site for the understanding of Neanderthals' behavior before their disappearance (Barroso et al., 2003; Barroso & Lumley, 2006). Sixteen Neanderthal remains were recovered in archaeostratigraphic units UE and UG at a depth of between 160 and 240 cm with notably the presence of a well preserved femur and a complete Neanderthal mandible: 11 in the Sala de Entrada (2 mandibles, 3 femurs, 1 tibia, 1 scapula, 1 phalanx, 1 rib, 1 pubis, and 1 tooth) and 5 in the Sala del Fondo (4 teeth and 1 humerus). An oval shaped hearth in zone Q18 of the Sala de Entrada at an average depth of - 234 cm was identified. It contained 32 fragments of Neanderthal burnt bones corresponding to a partial mandible, two femurs and a tibia, and a scapula. These burned elements associated with charcoals and faunal

remains were subject to fracture and defleshing and represent evidence of cannibal human actions. The climate according to ecological analyses (Barroso & Lumley, 2006:763) shows a succession of variable humid episodes in a rather cool temperate Mediterranean context.

The Middle Palaeolithic industry is composed of 813 pieces and correspond to a typical Mousterian with abundant recurrent "centripète" Levallois debitage (index = 36.5), low Mousterian type laminar index (8.10%) and absence of hand-axes. Out of 164 retouched tools, side-scrapers are the most numerous (39.6%) followed by notches (18.90%) and denticulates (11%) with the presence of 4 beautiful Mousterian points and a low number (5%) of Upper Palaeolithic type tools (burins, piercers).

With regards to the chronology of Neanderthal occupation in Zafarraya, a biostratigraphic study of small mammals in Mousterian levels (Barroso et al., 1983) suggested a late Mousterian presence. This was confirmed (Hublin et al., 1995) by  $C^{14}$  dating of  $29,600 \pm 600$  in the most recent Mousterian levels and U-Th dates showing an age of  $33,400 \pm 200$  for level associated with Neanderthal remains. However, these results were invalidated by new dates associated to the Zafarraya 2 mandible obtained by different methods (Michel et al., 2003) as follows: U-Th gamma: convergence zone between 42,000 and 50,000, U-Th alpha: 48,000 (-5100/+5400), U-Th TIMS:  $65,125 \pm 7,953$ ,  $C^{14}$ :  $36,900 \pm 3,000$  and AAR: 53,528. Michel et al. (2006, 2011) corroborate the fact that the results of the later studies point to a range of ages of between 35 to 50 ka for the Mousterian levels associated with the Zafarraya Neanderthal fossils while a recent  $C^{14}$  study (Wood et al., 2013) put the age of the

remains closer to the limit of this dating method of approximately 50 ka. These later results raise anew the issue of the late survival of the Neanderthals in the South of the Iberian Peninsula as also suggested by a recent genetic study (Dalen *et al.*, 2012).

## **Material and methods**

A rich faunal assemblage has been unearthed in the cave of Zafarraya out of which seventeen species have been identified from the list of 3,394 identifiable large mammal bone elements (Table 1). The conservation among carnivores species allow to separate them into two groups: scarce carnivores (*Vulpes vulpes*, *Ursus arctos*, *Crocuta crocuta*, *Lynx pardina*, *Felis silvestris*, *Mustela ermine* and *Mustela nivalis*) and well documented species such as *Panthera pardus* (7.22 %) and *Cuon alpinus* (5.45 %). *Capra pyrenaica* elements (78.37 %) are the most numerous and are found uniformly throughout the stratigraphy while *Rupicapra* presence is rather limited (1.44 %). *Bos primigenius*, *Equus ferus* and *hydruntinus*, *Sus scrofa*, and in larger proportion, *Cervus elaphus* (2.74 %), species roaming at some distance, were also brought into the cave.

The detailed published taphonomic study (Barroso & Lumley, 2006:775) covers the diverse types of bone conservation evidenced in the carnivore and large herbivore faunal assemblage, as well as a detailed analysis of bone surface modifications undertaken according to professionally recognized standards. The various categories of surface modifications are as follows: natural surface alterations (dissolution cupules, partial desquamation and total desquamation) and natural cracks, traces from carnivore action (cupules and

striae, ingested bones, cylinders and coprolites) and traces from anthropic action (notches, fractures, flakes, striae and burnt bones). Table 2 synthesizes qualitatively these surface modifications on large herbivore bone remains made by carnivores and Neanderthals, and are summarized as follows:

- *Capra*. All the different parts of the carcasses of *Capra* have been identified in the assemblage and the remains of this most abundant species have been subject to all the standard types of carnivore and humans actions. The number of anthropic bone modifications are not as numerous as those of carnivores and are concentrated on desarticulation of shoulders, elbows and feet, fracture on fresh bones, particularly femurs and tibias, and de-fleshing cut-marks on the axial skeleton i.e. ribs and vertebrae. It would appear that Neanderthals consumed essentially juveniles and adult females, characteristic of a hunt in the immediate surroundings of the cave. A certain number of bones have been repeatedly burnt, particularly in the hearth in the Sala de Entrada. Carnivores have left numerous cupules associated with comet shaped striae on distal and proximal bone extremities. The type of predation of *Capra* varies in the stratigraphic levels rich in carnivore remains: juveniles are more present in beds dominated by *Cuon*, while where *Panthera* is present adult preys are more numerous and the proportion of young specimens is lower. The main issue faced with regard to *Capra* is whether both carnivore and human predators competed directly for the primary access to this food resource, or whether one of the two dominated the environment in such a way that the kills were contributed by one and the other had secondary access to the already exploited carcasses.

Table 1. Identified large mammals bone elements (NR).

TAXA	NR	%
<b>Carnivora</b>		
<i>Cuon alpinus</i>	185	5.45
<i>Vulpes vulpes</i>	4	0.12
<i>Ursus arctos</i>	34	1
<i>Crocuta crocuta</i>	15	0.44
<i>Felis silvestris</i>	35	1.03
<i>Lynx pardina</i>	33	0.97
<i>Panthera pardus</i>	245	7.22
<i>Mustela erminea</i>	1	0.03
<i>Mustela nivalis</i>	8	0.24
<b>Artiodactyla</b>		
<i>Cervus elaphus</i>	93	2.74
<i>Capra pyrenaica</i>	2660	78.37
<i>Rupicapra rupicapra</i>	49	1.44
<i>Bos primigenius</i>	12	0.35
<i>Sus scrofa</i>	7	0.21
<b>Perissodactyla</b>		
<i>Equus caballus</i>	7	0.21
<i>Equus hydruntinus</i>	6	0.18
<b>TOTAL</b>	3394	100.00

- *Cervus*. All the long bones, scapulas and most of the mandibles of this species have been intentionally fractured following breakage patterns diagnostic of anthropic actions such as disarticulation or removal of tendons, without any sign of carnivore alteration. Most of the long bones and in particular femurs and tibias show striae of de-fleshing made by human cutting tools. The overwhelming anthropic bone modifications of *Cervus* contrast with the scarce exploitation of these remains by carnivores as evidenced by very few cupules. With regard to cervids, anthropic actions coincide with major lithic accumulations.

- *Rupicapra*. Overall traces are few since long bones are scarce. Whatever fractures are apparent seem to be from trampling. There are a few gnawing traces from small carnivores and cupule marks from large carnivores with two phalanxes showing signs of having been ingested by carnivores. It would seem that hunting of this species by Neanderthals may be excluded since no anthropic marks were found.

- *Bos*. All the bones of this species have been fractured mainly with spiral breaks on fresh bone typical of anthropic intervention. Several bones show linear anthropic striae diagnostic of cut-marks, with one humerus evidencing distally striae and cupules characteristic of carnivore activity on cartilaginous parts.

- *Equidae*. Most of the equid bones have been fractured further to violent impact on fresh bone after the animal death. Traces are apparent on all the bones. There are cut-marks of anthropic origins showing that humans removed muscles and consumed the meat, and evidence that carnivores acted on most of the

Taxon	Carnivore		Anthropic	
	Fractures	Traces	Fractures	Traces
<i>Capra</i>	+	+	+	+
<i>Cervus</i>		ε	+	+
<i>Rupicapra</i>		+		
<i>Bos</i>		+	+	+
Equidae		+	+	+
<i>Sus</i>		ε?	ε?	ε?

Table 2. Qualitative actions of predators on large herbivores.

material with traces of gnawing and cupules made posterior to breakage.

- *Sus*. Traces are scarce and fractures insignificant which render difficult to identify the type of predation this species was subject to.

Traces observed on carnivore bones are few, 12% of NR out of which a large proportion represents fractures due to trampling. Anthropogenic action on carnivore bones is rare with a few exceptions such as a fractured *Ursus* canine due to a violent hit, and burnt *Ursus* and *Lynx* canines. There is scarce evidence of action of carnivores on carnivore bones, with a few examples such as: cupules from carnivore teeth on *Ursus*, juvenile *Hyena* and *Cuon* bones, gnawing on *Lynx* bone and digested *Cuon* and *Lynx* phalanxes.

Neanderthal/carnivore competition for animal resources in the cave of Zafarraya surroundings is driven to a large extent by the geomorphology of the environment which affects the abundance and ease of access to prey, and thus the type of predation. Given the fact that the distance from the cave to available prey and the difficulty of transport will affect the type of accumulation and relative abundance of herbivore carcasses found in the site, we will define the nature of the favored foraging areas of the large herbivores and carnivores under study (Table 3).

Whether statistically there is a causal relationship between the presence of predators (carnivores or Neanderthals) and prey (large herbivores) in the site needs to be ascertained. We will try to correlate along the stratigraphy the number of herbivores elements with on one hand carnivore remains, and on

the other hand a proxy of Neanderthal occupation represented by the vertical distribution of lithic artifacts along the sequence. These faunal and lithic series are graphically presented in Figure 2 and will be the object of path analyses.

On the basis of the qualitative taphonomic observations (Table 2), the favored herbivore/carnivore foraging areas and proximity to the cave (Table 3), and the path analyses, we will suggest some inferred scenarios regarding the interaction between the two sets of predators, Neanderthals and carnivores, particularly as it relates to *C. pyrenaica*, *C.elaphus* and *R. rupicapra*.

## **Results**

### *1. Favored foraging areas*

The overwhelming number of *C. pyrenaica* elements (78.37 % of the assemblage), the occasional presence of other large herbivore remains and the limited number of carnivore carcasses from *P. pardus* and *C. alpinus* would indicate that the difference in conservation between well represented species and other identified less abundant species in the site, is related to the manner by which these remains were introduced in the cave. This differential conservation to a great extent is linked to the natural habitat(s) where the various species were roaming in the highly diverse geo-morphological landscapes surrounding the cave. An assessment of the favored foraging areas of the large herbivores in the proximate surroundings of the cave ought to be particularly informative with regard to the availability of prey as a function of distance

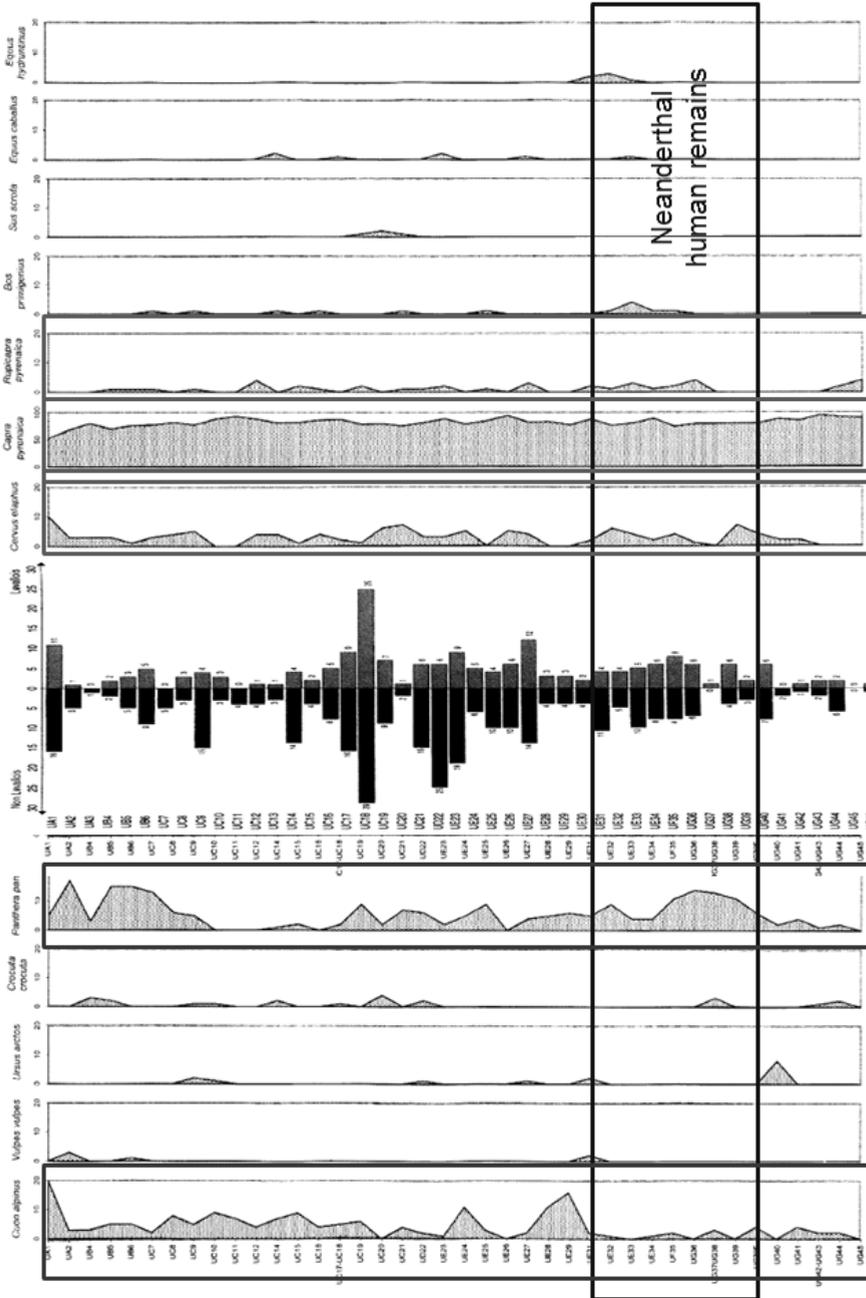


Figure 2. Distribution of large herbivore and carnivore remains and retouched lithic artifacts along the stratigraphy.

from the cave to these natural habitats. The cave of Zafarraya benefits of a unique strategic position (Figure 1) with access to three diverse biotopes with their related faunas. Its paleo-environment may be divided into three ecological domains: 1) the limestone escarpment with the rupicolous steep rocky terrain in the immediate vicinity of the cave and neighboring steep slopes of the surrounding sierras, 2) the southern sloping forested hills leading to the Mediterranean coast, and 3) the lush open and forested space of the polje to the north of the pass of the Boquete de Zafarraya with rich hydrological resources collected from the surrounding sierras. On the basis of the species ecological affinities (Barroso & Lumley, 2006:765), it is possible to assign the herbivore and carnivore species under study to these three identified ecological domains. This assignment is illustrated in Table 3 and defines the favored foraging areas of the herbivores and carnivores found in the site. It provides qualitatively at a glance an estimate of the relative distance predator to available prey and difficulty of transport of carcasses, two factors that should help in evaluating the origin, types and abundance of elements found in the site.

## *2. Path analyses*

The site of Zafarraya offers a unique opportunity to correlate a continuous series of lithic artifacts in the sedimentary sequence to the stratigraphic distribution of carnivore and faunal elements of the archaeostratigraphic units as illustrated in Figure 2. The Mousterian lithic artifact series will be used as a proxy for Neanderthal presence in the cave (Monclova, 2010), and only the five main faunal species with sufficient significant

data will be covered. The degree of association between pairs of accumulation variables as expressed by the correlation coefficients of the lithic and faunal series is summarized in Table 4.

Unlike regression analysis where one tries to describe the functional relationship between, and/ or predict, one variable in terms of one or several others, correlation analysis serves to determine whether two variables are interdependent or co-vary without asserting a causal relationship between them (Sokal & Rohlf, 2012). A multiple regression with independent variables such as for example lithic and carnivore elements could be used to explain herbivore accumulation, the dependent variable. However, the main drawback of multiple regressions is that it assumes that the independent variables are direct unrelated causes of the dependent variable, disregarding the indirect causal relationship that might exist between them. Path analysis developed by Sewall Wright (1968), a population geneticist, is a powerful statistical technique considered as an extension of multiple-regression that takes into account the effects of correlated independent variables. Therefore, we will use a path analysis to infer the causal relationships between the herbivore prey accumulations and the presence of accumulators (carnivores and Neanderthals) in the cave of Zafarraya after taking into account the reciprocal influence of the accumulator variables.

Path analysis may be depicted by a structural model represented by a path diagram where causal relationships are illustrated as headed arrows. Instead of independent and dependent variables the respective terms of predictors and criterion are used. There are two basic conventions: a single-headed arrow points from cause (predictor) to effect

Table 3. Favored foraging areas of Zafarraya fauna.

	(1) Zafarraya cave w. steep slope environment	(2) Zafarraya southern sloping hills	(3) Polje north of Zafarraya pass		
	Rupicolous	Rupicolous with forest affinity	Forest	Grove/Marshes	Prairie
<b>HERBIVORES</b>	<i>C. pyrenaica</i>  <i>R. rupicapra</i>	<i>C. elaphus</i> <i>R. rupicapra</i>  <i>S. scrofa</i>	<i>C. elaphus</i>  <i>S. scrofa</i>	<i>B. primigenius</i> <i>S. scrofa</i>	<i>E. caballus</i> <i>E. hydruntinus</i>
<b>CARNIVORES</b>	<i>P. pardus</i> <i>C. alpinus</i> <i>V. vulpes</i>	<i>P. pardus</i> <i>C. alpinus</i> <i>V. vulpes</i> <i>U. arctos</i>  <i>C. crocuta</i>	<i>P. pardus</i> <i>C. alpinus</i> <i>V. vulpes</i> <i>U. arctos</i> <i>F. silvestris</i> <i>L. pardina</i> <i>C. crocuta</i>	<i>P. pardus</i> <i>C. alpinus</i> <i>V. vulpes</i> <i>U. arctos</i> <i>F. silvestris</i> <i>L. pardina</i> <i>C. crocuta</i>	<i>C. alpinus</i> <i>V. vulpes</i>

(criterion), while a double-headed curved arrow indicates that predictors are merely correlated with no causal relations assumed. The measured numerical data of the predictors are allocated to different levels of influence in a sequential order, where earlier levels affect the subsequent ones and not the reverse. The strength of the influence is described by path coefficients which are standard partial regression coefficients. Numerically, path analysis represents a continuous sequence of multiple correlation calculations (that follows the cascade of influences) from a correlation matrix as input data. In addition to the path coefficients, partial correlation coefficients between the predictors at the same levels are computed to ascertain the common influences not explained by the model.

On the basis of the correlation coefficients of Table 4 we have conducted

four path analyses to try to shed some light on the relative influence of the main carnivore predators and Neanderthals on herbivore bone accumulations. The computations of these four sequential models were performed with the path analysis statistical software made available online by StatTools ([http://www.stattools.net/Path\\_Pgm.php](http://www.stattools.net/Path_Pgm.php)). The results of the four path analysis models are as follows:

A) *General model: carnivore and lithic predictors, and herbivore criterion.* The total carnivore (*P. pardus* + *C. alpinus* + *V. Vulpes* + *U. arctos* + *C. crocuta* + *F. silvestris* + *L. pardina*) and large herbivore elements (*C. pyrenaica* + *C. elaphus* + *R. rupicapra* + *S. scrofa* + *B. primigenius* + *E. caballus*/*E. hydruntinus*) as well as the number of lithic artefacts were used to compute the path coefficients of Figure 3. A multiple regression

Correlation coefficients	Carnivores	Lithics	Herbivores	Correlation coefficients	<i>Panthera</i>	<i>Cuon</i>	Lithics	<i>Capra</i>	<i>Cervus</i>	<i>Rupicapra</i>
Carnivores	1			<i>Panthera</i>	1					
Lithics	0.3965405	1		<i>Cuon</i>	0.1783097	1				
Herbivores	0.7116173	0.5583822	1	Lithics	0.1578367	0.5446315	1			
				<i>Capra</i>	0.5614857	0.4731471	0.5525579	1		
				<i>Cervus</i>	0.386692	0.3060298	0.484954	0.5901054	1	
				<i>Rupicapra</i>	0.4712966	-0.098326	0.1765506	0.4745061	0.4170479	1

Table 4. Correlation coefficients of faunal elements and lithic artifacts time series.

was run showing a significant multiple regression coefficient of 0.773 between herbivores as dependent variable and carnivores and lithics as independent variables.

B) *C. pyrenaica model*: *P. pardus*, *C. alpinus* and lithic predictors, and *C. pyrenaica criterion*. We have selected a unidirectional compound path model to explore the relative causal effects that the most present predators in the site, *Panthera*, *Cuon* and Neanderthals, had on the most abundant bone accumulation of *Capra* (78.37 % of the assemblage). There are multiple ways of positioning the variables into a path diagram. We will use a model where we assume that the accumulation of *Capra* remains by the two main carnivore predators (*Panthera*, *Cuon*) is affected by the presence of humans (lithics) to compute the path coefficients (Figure 4). The other two model possibilities would be to test the effect of *Cuon* on *Panthera* and human (lithics) accumulations or *Panthera* on the accumulation of *Cuon* and human (lithics) accumulations. A multiple regression was run showing a significant multiple regression coefficient of 0.748 between *Capra* as dependent variable and *Panthera*, *Cuon* and lithics as independent variables. Table 5 shows the computation of the direct and indirect effects of the predictors (predators) on the criterion (accumulated prey).

C) *C. elaphus model*: *P. pardus*, *C. alpinus* and lithic predictors, and *C. elaphus criterion*. This model will use the same unidirectional compound path to explore the causal effects related to the accumulation of *Cervus* remains which represent 2.74 % of the faunal assemblage. The model assumes that the accumulation of *Cervus* by the two main carnivore predators (*Panthera*, *Cuon*) is affected by the presence of humans (lithics) to compute the path coefficients

(Figure 5). A multiple regression was run showing a less significant multiple regression coefficient of 0.578 between *Cervus* as dependent variable and *Panthera*, *Cuon* and lithics as independent variables, which is explained in part by the low number of elements of this species found in the site.

D) *R. rupicapra* model: *P. pardus*, *C. alpinus* and lithic predictors, and *R. rupicapra* criterion. As for the two previous models, we use here the same unidirectional compound path to explore the causal effects related to the accumulation of *Rupicapra* remains which represent 1.44 % of the faunal assemblage, a relatively low percentage. The model assumes that the accumulation of *Rupicapra* by the two main carnivore predators (*Panthera*, *Cuon*) is affected by the presence of humans (lithics) to compute the path coefficients (Figure 6). A multiple regression shows a low significant multiple regression coefficient of 0.56 between *Rupicapra* as dependent variable and *Panthera*, *Cuon* and lithics as independent variables.

## Discussion

Optimal foraging theory OFT (MacArthur & Pianka, 1966) has been used to estimate quantitatively catchment areas of archaeological sites showing that “surroundings of a site are a determining influence on the faunal composition of the archaeological deposits (i.e. that hunting specialization at a particular site depends on the topographic characteristics of the area in which it is located)” (Marín Arroyo, 2009). This assertion supports our assignment of the fauna found in the site to the three geomorphological domains in the surroundings of the cave (Table 3) in function of the favored foraging area criterion. This assignment calls for some

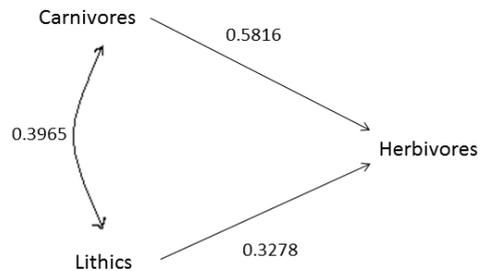


Figure 3. Path diagram of carnivore + lithic predictors and herbivore criterion.

observations with regard to distance from the cave to the herbivore foraging areas and ease of access to prey by predators. The herbivore trophic significance (i.e. food chain attractiveness for predators) may be associated to the distance from the cave (where remains were deposited) to their favored foraging environment and to the geomorphology surroundings of the cave as follows:

- High trophic significance (short distance): *C. pyrenaica* → immediate steep cave environment; *R. rupicapra* → immediate steep cave environment & southern sloping hills.
- Medium trophic significance (intermediate/far distance): *C. elaphus* → southern sloping hills & forest in polje.
- Low trophic significance (far distance): *S. scrofa*, *B. primigenius*, *E. caballus*/*E. hydruntinus* → forest, grove/marshes, prairie in polje.

*C. pyrenaica*, the most abundant herbivore in the site is fully adapted to the steep slopes of this region and is to be seen still today in the Sierra de Alhama, its favored environment. The immediate rocky nature of the surroundings of the cave is to a great

Figure 4. Path diagram of *P. pardus* + *C. alpinus* + lithic predictors and *C. pyrenaica* criterion.

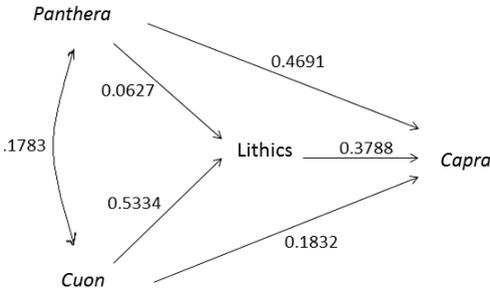
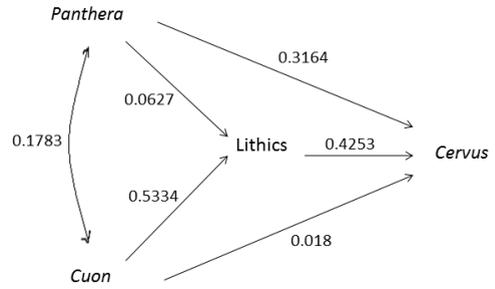


Figure 5. Path diagram of *P. pardus* + *C. alpinus* + lithic predictors and *C. elaphus* criterion.



extent its exclusive and sole ecological niche compared to other large herbivores. If the main criterion of predation is the short distance to available prey, it is most probable that *Capra* occupied the highest trophic position for immediate predators such as specialized Mousterian hunters, and *P. pardus* and *C. alpinus*. These two carnivore species are fully adapted to this rupicolous terrain (Hayward *et al.*, 2006; Johnsingh, 1985) and presently share the same habitat (Wang & Macdonald, 2009; Venkataraman, 1995). *C. elaphus*, the second most numerous herbivore is characteristic of forest cover and probably foraged away from the cave in the southern forested hills and the wooded environment of

the polje, which would mean that, given the greater distance to the cave and its rock-strewn access, humans were more likely to have transported these remains to the cave than the carnivores. *R. rupicapra*, the third most prevalent prey found in the site moves occasionally in the same steep environment as *C. pyrenaica*, particularly in summer after giving birth, but takes refuge in forested hills during severe winters (Bon *et al.*, 2007; Darmon *et al.*, 2012). Its remains show marks attributed to carnivores and almost no anthropic actions. The presence of the other large herbivores *B. primigenius* and *E. caballus/E. hydruntinus* is insignificant in the site, which might not be surprising since according to our

	Direct effect	Indirect effect	Total effect
<i>Panthera</i> → Lithics → <i>Capra</i>	0.4691	0.0627 x 0.3788 = 0.0238	0.4929
<i>Cuon</i> → Lithics → <i>Capra</i>	0.1832	0.5334 x 0.3788 = 0.2021	0.3853
<i>Panthera</i> → Lithics → <i>Cervus</i>	0.3164	0.0627 x 0.4253 = 0.0267	0.3431
<i>Cuon</i> → Lithics → <i>Cervus</i>	0.0180	0.5334 x 0.4253 = 0.2269	0.2449
<i>Panthera</i> → Lithics → <i>Rupicapra</i>	0.4870	.06270 x 0.2851 = 0.0179	0.5049
<i>Cuon</i> → Lithics → <i>Rupicapra</i>	-0.3404	0.5334 x 0.2851 = 0.1521	-0.1883

Table 5. Direct and indirect effects of predictors (predators) on criterion (accumulated prey).

topography related favored foraging area allocation (Table 3), they roamed at a significant distance from the cave in the polje. For these species, we may suggest that the transport of their carcasses by carnivores was most challenging given their weight, the distance to the cave and the very steep nature of the slopes leading to the cave. These transport factors and the fact that only anthropic marks on mainly adult subjects were observed, would point towards predation by humans for these species, and secondary access by carnivores if any.

Looking at the correlations coefficients of Table 4, there is a greater significant association between the presence of carnivores and herbivores elements in the cave (0.712) than between lithics (Neanderthals) and herbivores (0.558), whereas the joint presence of Neanderthals (lithics) and carnivores is rather weak (0.397), which would seem reasonable since the occupation of these two predatory groups must have occurred in an alternating mode. One could infer from the difference in correlation ( $0.712 - 0.558 = 0.154$ ) that the carnivores were much more active in bringing herbivores carcasses to the cave than Neanderthals. However, this general inference needs to be clarified in light of the fact that *C.*

*pyrenaica* elements represent 78.37 % of the faunal assemblage. Taking into account the three herbivores with the most significant representation, the co-variation associating main predators and the main herbivores may be summarized as follows:

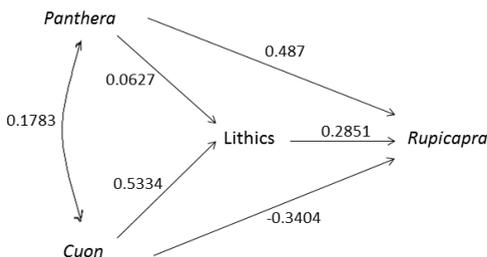
- The association between *C. pyrenaica* elements and *Panthera* (0.561) on one hand, and with Neanderthals (0.553) on the other, is significant but closely identical, while it is slightly inferior with *Cuon* (0.473). This does not clarify which predators were the unequivocal main contributors to this bone accumulation.
- *C. elaphus*, has a greater association (0.485) with Neanderthals (lithics) than with *Panthera* (0.387) or *Cuon* (0.306).
- While the association of *R. rupicapra* with *Panthera* is weak (0.471), it is practically insignificant with Neanderthals (0.177) and nil with *Cuon* (-0.098). This seems to corroborate the observation that the remains of *R. rupicapra* show marks attributed to carnivores, probably *Panthera*, and very little anthropic actions.

These correlations between predators and herbivore prey in the site do not allow to infer directly causes and effects between these time dependent variables of element accumulation, namely which of the carnivores or Neanderthals were the main contributors to these faunal assemblages. This is the reason why we turned to path analyses.

The path analyses call for the following comments related to the four models analyzed:

*Path diagram of carnivore + lithic predictors and herbivore criterion:* The results of the path analysis summarized in Figure 3 show

Figure 6. Path diagram of *P. pardus* + *C. alpinus* + lithic predictors and *R. rupicapra* criterion.



the low non-causal correlation 0.3965 between carnivores and lithics, and the much greater direct effect that carnivores had on overall herbivore accumulation (0.5816) as compared to a much lower contribution by Neanderthals/lithics (0.328). This might be interpreted as an indication that the cave was a carnivore den occasionally occupied by Neanderthals, and thus that the herbivore bone assemblage was in a greater part contributed by carnivores.

*Path diagram of P. pardus + C. alpinus + lithic predictors and C.pyrenaica criterion:* A cursory look at the correlation (Table 4) of *Capra* with *Panthera* (0.562), not too far off from the one with lithics (0.553) but greater than the one with *Cuon* (0.473), could imply that these predators had approximately more or less equivalent influence on *Capra* accumulation. However, the path coefficients in Fig.4 show that the direct influence of *Panthera* (0.4691) on *Capra* accumulation is greater than lithics (0.3788) and substantially more important than *Cuon* (0.1832). The indirect effect (Table 5) due to the human presence is insignificant in the case of *Panthera* (0.0238); a possible interpretation being that *Panthera* and Neanderthals did not compete in hunting *Capra* and transporting its carcasses to the site due to alternate period of occupations as evidenced by the low correlation between them (0.158). On the contrary, the indirect effect due to the human presence is significant in the case of *Cuon* (0.2021), which could mean that *Cuon* had a relatively important secondary access to *Capra* carcasses brought in by humans when these occupied the cave, with the possibility that Neanderthals might have consumed *Cuon* in light of the appreciable correlation that exists between them (0.545). This would not be the case with *Panthera*'s accumulation given the low correlation

between *Panthera* and *Cuon* (0.1783) which points towards an alternating occupation of the cave by these two carnivores. It is worth highlighting that the two carnivores had 72%  $(0.4691+0.1832/0.3788)$  more direct relative weight in explaining this bone assemblage than Neanderthals.

*Path diagram of P. pardus + C. alpinus + lithic predictors and C.elaphus criterion:* In Figure 5 the first two levels (correlation between *Panthera* and *Cuon*, and indirect influence of the carnivores) are identical to the previous *C.pyrenaica* model (Figure 4). The most important direct effect contributor to *Cervus* bone accumulation is lithics, i.e. Neanderthals (0.4253) followed by *Panthera* (0.3164) while the influence of *Cuon* (0.018) is practically nil. The indirect effect of *Panthera* accumulation of *Cervus* (0.0267) due to the human presence is quasi-inexistent, while on the contrary the indirect effect of accumulation of *Cervus* by *Cuon* due to the human presence is again significant (0.2269). A possible explanation might be that *Cuon* had a relatively important secondary access to *Cervus* carcasses brought in by humans. The greater direct effect of Neanderthals on *Cervus* accumulation compared to *Panthera* might be explained by the fact that this species foraged at some distance from the cave in the southern sloping hills and forest of the polje and transport of its carcasses to the site by carnivores would have been difficult given the steep and arduous path to the cave. We may thus infer that *Cervus* was hunted and transported to the cave for consumption primarily by Neanderthals, and scavenged by *Cuon* given its quasi nil direct effect and high indirect effect, and plausibly by *Panthera*, if we take into account the fact that the taphonomic study (Barroso & Lumley, 2006) demonstrates the

scarce exploitation of these remains by carnivores as evidenced by the very few cupules on *Cervus* bone surfaces, and evidence of occasional scavenging of young specimens by *Panthera*.

*Path diagram of P. pardus + C. alpinus + lithic predictors and R. rupicapra criterion.*

In Figure.6 the first two levels (correlation between *Panthera* and *Cuon*, and indirect influence of the carnivores) are identical to the *C.pyrenaica* model (Figure 4). The most important direct effect contributor to *Rupicapra* bone accumulation is *Panthera* (0.487) whose influence is almost double than the one from Neanderthals/lithics (0.2851). The path coefficient between *Cuon* and *Rupicapra* (-0.3404) is negative for computational reason, since the correlation between these two variables (-0.098326) is the sum of the products of the chains of path coefficients or correlations along all the paths by which they are connected. This negative direct effect might be due to the higher weight of non-causal exogenous effects. The indirect effect of *Panthera* accumulation of *Rupicapra* (0.0179) due to the human presence is insignificant, while on the contrary the indirect effect of accumulation of *Rupicapra* by *Cuon* due to the human presence (0.1521) is appreciable and decreases the total causal effect to -0.1883 which means that *Cuon* had a small negative effect on *Rupicapra* accumulation. The much greater direct influence of *Panthera* on *Rupicapra* accumulation (0.487) than Neanderthals' (0.2851) is consistent with the one found in the *Capra* model which might be rationalized by the fact that *Rupicapra* is a species fully adapted to the rupicolous terrain surrounding the cave where *Panthera* ruled the predatory environment.

The general model of the path analysis highlighted the much greater influence that carnivores had on the overall herbivore

accumulation in comparison with the lower human contribution. However, a breakdown of the general path analysis into the three main prey analyses shows the varying influence that the two main carnivores, *Panthera* and *Cuon*, had on the three most represented herbivores, *Capra*, *Rupicapra* and *C. elaphus*

*Panthera* was definitely the main predator of *Capra* and *Rupicapra* in Zafarraya as shown by the path analyses. With regard to *Capra* it is evident from the direct effect path coefficient (0.4691), compared to Mousterian lithics (0.378), that *Panthera* was the main accumulator of this species. This inference is confirmed in light of the more numerous modifications it inflicted on bone surfaces. It is a most realistic interpretation considering its versatility in the immediate rock-strewn rupicolous environment of the cave. The main issue is whether *Panthera* and humans competed directly for the primary access to *Capra*, or in other words whether one of the two dominated in such a way that the kills were contributed by one and the other had secondary access to the already exploited carcasses. The insignificant indirect effect due to the human presence in the case of *Panthera* (0.0238) and the low correlation between them (0.158) would favor the rejection of this hypothesis of direct competition; thus, the presence of these two predators was most probably mutually exclusive, i.e. when one was present the other was absent and the occupation of the cave was carried out in an alternating mode. Whether there was occasional scavenging by either predator is a possibility in light of the existence of surface modifications by both carnivores and Neanderthals on a certain proportion of remains. Affirming categorically which of the predator scavenged systematically is fraught with uncertainty due to the complex superimposition of the modification processes.

For *Rupicapra* one could advance the inference that *Panthera* was the overwhelming accumulator based on its direct path coefficient (0.487) which is almost double than the one from lithics/Neanderthals (0.2851) i.e. hunting of this species by Neanderthals was extremely rare as evidenced by the almost non-existent anthropic actions observed on its remains. There was a negative direct effect on *Rupicapra* accumulation by *Cuon* (-0.3404) dampened by a positive indirect effect (0.1521) from human presence which might be construed as *Cuon* being the last species to take advantage of *Rupicapra* carcasses given the domination of *Panthera* and the lesser role of humans in exploiting these remains.

The remains of *C. elaphus*, a species foraging in the forests of the southern sloping hills and polje at some distance from the cave, show substantial anthropic fractures and intense surface modifications with scarce exploitation by carnivores. As shown in Figure 5, this concurs with the greater lithics direct effect path coefficient (0.4253) compared to *Panthera* (0.3164) and *Cuon* (0.018), and the low indirect effect of *Panthera* due to human presence (0.0267). It confirms that Neanderthals were the principal accumulator of *C. elaphus*, particularly considering the difficulty of transport of carcasses to the site by carnivores due to the steep nature of the rock-strewn abrupt terrain. It is most probable that, in light of the quasi nil direct effect (0.018), appreciable indirect effect due to human presence (0.2269) of *Cuon* and the very few carnivore surface modifications, that this species might have scavenged the *Cervus* remains procured by Neanderthals.

Finally, most noticeable is the low or inverse contribution of *Cuon* to caprid accumulations (direct effect of 0.1832 and -0.3404) and particularly to *Cervus* (0.018)

compared to other prehistoric sites where small bovids are its favored prey (Karanth & Sunquist, 2000; Cohen, 1978). This might be explained by the fact that *Cuon* was at a competitive disadvantage when confronted with *Panthera* as evidenced by the low presence correlation with *Panthera* (0.1783), the dominating accumulator. It might even itself have been the target of predators as shown by digested *Cuon* phalanges and tooth marks on various bones. Although *Cuon* intervened on some of *Capra* remains it is not apparent that it might have been the originator in the transport of carcasses, and the questions remains whether it had primary or secondary access to the carcasses, particularly considering that its association with the presence of humans, as indicated by the correlation with lithics of 0.545, is significant.

## Conclusions

Drawing on the extensive published taphonomic and zooarcheological studies (Barroso *et al.*, 2003; Barroso & Lumley, 2006), a statistical path analysis associated to topographic ecological considerations has allowed us to shed further light on Neanderthal/carnivore occupation overlap in the cave of Zafarraya, and how these two sets of predators interacted for the nutritional resources of herbivore elements, and in particular *C. pyrenaica*. At first glance the applicable scenario seems to be that in the immediate surroundings of the cave, Neanderthal niche overlap with carnivores is complete and Neanderthals were not able to exclude them from the nearby ecological environment, this resulting in their coexistence. However, the main findings put in doubt the validity of this scenario for the following reasons:

- *Capra*, the favored prey with continuous presence, was hunted by both Neanderthals and carnivores in the immediate cave surroundings. However, *Panthera* was definitely the main predator as shown by the archaeological record and path analyses, and its presence with Neanderthals was not coincidental but most probably mutually exclusive, i.e. when one was present the other was absent and the occupation of the cave was carried out in an alternating mode.
- For *Rupicapra* the inference is that *Panthera* was the overwhelming accumulator and hunting of this species by Neanderthals was extremely rare, if not nil.
- Neanderthals were the principal accumulator of *C. elaphus* which foraged at some distance from the cave, and in light of the very few carnivore surface modifications, it is most probable that carnivore scavenged *Cervus* remains procured by Neanderthals.
- The other large herbivores *B. primigenius* and *E. caballus/E. hydruntinus* which foraged at a distance in the polje show only anthropic marks on mainly adult subjects which point towards predation by humans with secondary access by carnivores, if any.

These findings may be viewed in the context of the two-species Lotka-Volterra competition model for resources (Chesson & Kuang, 2008) which stipulates that when niche overlap is complete the species with the larger fitness excludes the other, and as niche overlap decreases the degree of coexistence increases as the ratio of fitness of the two species decreases. This model has been applied to ecologically based definition of seasons to clarify predator-prey interactions in mammal communities

(Basille *et al.*, 2012). In the immediate surroundings of the cave it is clear that the fitness of *Panthera* was greater than Neanderthals' and therefore when *Panthera* was present it excluded Neanderthals as evidenced by the record of *Capra* and *Rupicapra* remains. Further from the cave, in the southern hills and the polje where large herbivores roamed, Neanderthals had probably a greater fitness than carnivores due to their mobility and cooperative hunting skills, which also translate into the accumulation of remains of *C. elaphus* and other large herbivores from these foraging areas. If there was coexistence, it would be apparent when one or the other predator scavenged, which from a time prospective must have been short periods linked to seasonality, weather conditions and occupation randomness. Thus, we may conclude that in the case of Zafarraya, the archaeological record would indicate that the degree of fitness of the herbivore prey accumulators, be it carnivores or Neanderthals, was related to the nature of the three geomorphological domains in the vicinity of the cave and the favored foraging areas of hunted herbivores. We hope that further studies being undertaken will confirm and expand the results we have just exposed.

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