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Carrying Capacity, Available Meat and the Fossil Record of the Orce Sites (Baza Basin, Spain)

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Abstract: The Early Pleistocene sites of Orce in southeastern Spain, including Fuente Nueva-3 (FN3), Barranco León (BL) and Venta Micena (VM), provide important insights into the earliest hominin populations and Late Villafranchian large mammal communities. Dated to approximately 1.4 million years ago, FN3 and BL preserve abundant Oldowan tools, cut marks and a human primary tooth, indicating hominin activity. VM, approximately 1.6 million years old, is an outstanding site because it preserves an exceptionally rich assemblage of large mammals and predates the presence of hominins, providing a context for pre-human conditions in the region. Research suggests that both hominins and giant hyenas were essential to the accumulation of skeletal remains at FN3 and BL, with secondary access to meat resources exploited by saber-toothed felids. This aim of this study aims to correlate the relative abundance of large herbivores at these sites with their estimates of Carrying Capacity (CC) and Total Available Biomass (TAB) using the PSEco model, which incorporates survival and mortality profiles to estimate these parameters in paleoecosystems. Our results show: (i) similarities between quarries VM3 and VM4 and (ii) similarities of these quarries with BL-D (level D), suggesting a similar formation process; (iii) that the role of humans would be secondary in BL-D and FN3-LAL (Lower Archaeological Level), although with a greater human influence in FN3-LAL due to the greater presence of horses and small species; and (iv) that FN3-UAL (Upper Archaeological Level) shows similarities with the expected CC values for FN3/BL, consistent with a natural trap of quicksand scenario, where the large mammal species were trapped according to their abundance and body mass, as there is a greater presence of rhinos and mammoths due to the greater weight per unit area exerted by their legs. Given the usefulness of this approach, we propose to apply it first to sites that have been proposed to function as natural traps.

Keywords: prey biomass; large mammals; taphonomy; Early Pleistocene; Western Europe; Venta Micena; Fuente Nueva 3; Barranco León

1. Introduction

Reconstructing the ecological conditions under which past species evolved is of great interest, because it allows us to interpret how different aspects affected their evolution. Resource availability is among the parameters that most influence the distribution and survival of species. Animal resources played a key role in the survival of the human lineage since at least 2.5 million years ago (Ma) [1] and were particularly critical for Pleistocene hominins in Europe [2–4], although for some human species it has been suggested that they also consumed high amounts of plant resources [5–11]. Even today, most hunter-gatherer societies rely heavily on animal resources [12–14]. Many researchers have argued that large mammals were the primary source of meat and fat for hominins in the Pleistocene [3,11,15–22]. In this way, the study of the ecological framework in which hominin groups evolved can shed light on their subsistence strategies and patterns of resource exploitation, which are key to the study of human evolution [23–25].

In order to assess the ecological conditions of past large mammal communities, Carrying Capacity and meat availability can be used as indices useful for characterizing ecosystems and paleoecosystems (e.g., [26–32], among others). The term Carrying Capacity is widely used in the life sciences and is applied at a variety of levels of analysis, from molecular to ecological studies (see [33]). In present-day ecosystems, Carrying Capacity has been used to assess the status of large mammal populations and to guide management and conservation efforts [27–29]. Typically, these studies use the third meaning of Carrying Capacity as defined by Sayre [33], where K is the intrinsic population growth limit after long-term environmental stability. Applied to paleosynecology, it is useful for establishing predator–prey relationships derived from the obtaining of accurate biomass estimates [32,34–37]. In this study, as proposed by Coe et al. [26], we will consider Carrying Capacity (CC) as synonymous with the prey biomass species that can be sustained over time in an ecosystem. The concept of CC is sometimes used as a synonym for the availability of meat resources in ecosystems (e.g., [38,39]). However, CC (i.e., the total biomass of an ecosystem) cannot be used by the secondary consumers without leading the ecosystem to collapse. For this reason, we support the use of the term 'available meat' to refer to the biomass fraction of the ecosystem that can be sustainably used by the secondary consumers (see [30,37,40–45]). Therefore, we use the concept of available meat as the primary consumer biomass potentially available to the secondary consumers, which was termed Total Available Biomass (TAB) by Rodríguez-Gómez et al. [40].

In present-day ecosystems, CC estimates for large mammals are calculated from observed densities and average population weights, sometimes using three-quarters of adult female weight [27–29] and in other cases using adult female weight directly [31]. These approaches are not easy to apply in the case of paleoecosystems (see [37]) and alternatives have been sought, sometimes using average adult body masses (e.g., [35,46–52]; but see [37]) or estimating ecosystem Carrying Capacity from climatic parameters (e.g., [32,36,38,39]). Survival profiles are another alternative used to infer average population body mass [37], which allows for obtaining values similar to the Hatton et al. [31] approach using mean adult female body mass for current ecosystems. These survival profiles provide information on the proportion of individuals in a population who survive by age group and thus make it possible to obtain mortality profiles (i.e., the proportion of individuals who die by age group in the population). From these mortality profiles, if conditions of stability and stationarity are met (see [53,54]), it is then possible to estimate the long-term meat resources available in a paleoecosystem [30,37,40–45,55,56]. Leslie-Lewis matrices or the Weibull model are both useful tools for obtaining survival and mortality profiles, thus allowing for the estimation of age structures for fossil populations and modeling their dynamics [37,54,55,57]. We developed the PSEco model from estimates of survival and mortality profiles of herbivore species, which makes it possible to estimate ecosystem CC, TAB and secondary consumer biomass [45]. Results from this model on predator–prey biomass relationships resemble those found in current African ecosystems [45], supporting the use of this methodology.

Located about 150 km northeast of the city of Granada (SE Spain), in the eastern sector of the Guadix-Baza Depression and within the Baza Basin, the Orce sites are of great interest for the study of human evolution in Europe, since they provide information on the ecological conditions encountered by the first human settlers in Western Europe, as well as on the period preceding the first hominin dispersal in this area. The archaeological sites of Fuente Nueva-3 (FN3) and Barranco León (BL) preserve skeletal remains of 18 large mammalian species [58–61] (13 large prey, Table 1), as well as anthropic markings associated with Oldowan lithics (i.e., Mode 1) [22,62–68]. Using a combined approach based on biostratigraphy, magnetostratigraphy and electron spin resonance (ESR), the ages of BL and FN3 were estimated in 1.43 ± 0.38 Ma and 1.19 ± 0.21 Ma, respectively [66,69]. Additionally, cosmogenic nuclides yielded an age estimate of 1.50 ± 0.31 Ma for FN3 [70]. Currently, the oldest human fossil in Western Europe is a deciduous molar tooth of BL dated at ~1.4 Ma [66]. A marshy environment is associated with the excavated levels of BL, with the exception of level D, which has fluvial features and contains the majority of the archaeological assemblage [66]. The D level is subdivided into two layers, D1 and D2 and the time of its deposition was very short, which excludes it from being a palimpsest [66,71]. Two archaeological levels are grouped for the six layers of the fertile strata of FN3: a Lower Archaeological Level (LAL) (layers 1–3) and an Upper Archaeological Level (layers 4–6) [22,64,72,73], which do not differ in the composition of their faunal assemblages (see Table 1), except for the abundance of megaherbivores, and probably represent two very close temporal events. Further from Orce is also a key paleontological site for studying Early Pleistocene large mammal communities, Venta Micena (VM), which is slightly older biostratigraphically (1.6–1.5 Ma) than FN3 and BL and has no evidence of human presence (i.e., there are no lithic tools, anthropic marks on bones or human fossil remains from this site). However, it presents a huge amount of fossil remains from an excavation area of ~400 m^2 in several quarries of Venta Micena (e.g., VM2, VM3 and VM4), with more than 24,000 skeletal remains showing excellent preservation and low levels of weathering in more than 90% of the remains, which has allowed the identification of 21 species (14 large prey, Table 1). The role of scavenging hyenas was essential in the accumulation of these skeletal remains in the vicinity of their denning sites during a period of several years [74–76]. In contrast, Granados et al. [77] proposed a different interpretation of the Venta Micena paleontological layer, based on isotopic and geochemical studies. Their findings suggested that this layer was formed by a series of episodes of upward and downward expansion of a shallow lake that originated in the vicinity of the deposits. However, in a small sample excavated in quarry VM4, ~350 m away from VM3, Luzón et al. [78] proposed that a different carnivore than in VM3 participated with a key role in bone accumulation, arguing based on taphonomic differences between the two quarries (e.g., a lower weathering rate in VM4, more abundant articulated remains than in VM3 and less intensity of fractures and gnawing marks by the hyenas). In a later paper, however, Palmqvist et al. [79] demonstrated that the differences between these two quarries were not due to the intervention of different carnivores as bone accumulating agencies, but to differences in the time elapsed until the skeletal remains were covered by limestone sediments (this period was shorter in VM4, which explains the better preservation of the remains in this quarry compared to VM3).

Table 1. Minimum number of individuals (MNI) data from [22,68,78–80] of large herbivores identified in the faunal assemblages of the Orce sites (Granada, Spain) analyzed in this study, together with the relative percentage of abundance for each species. Abbreviations: VM: Venta Micena; BL: Barranco León; FN3: Fuente Nueva-3; UAL: Upper Archeological Level of FN3; LAL: Lower Archeological Level of FN3. * Remains showing gnaw marks made by a porcupine. [a] Palmqvist et al. [79]; [b] Espigares [80]; [c] Luzón et al. [78]; [d] Espigares et al. [22]; [e] Yravedra et al. [68].

Herbivore Species	VM3 [a,b]	VM4 [a,c]	FN3-UAL [d,e]	FN3-LAL [d,e]	BL-D [d]
Ammotragus europaeus					1 (2.1%)
Bison sp.	51 (17.3%)	3 (7.1%)	8 (11.9%)	3 (8.1%)	4 (8.3%)

Table 1. *Cont.*

Herbivore Species	VM3 ^{a,b}	VM4 ^{a,c}	FN3-UAL ^{d,e}	FN3-LAL ^{d,e}	BL-D ^{d}
Bovidae indet. (cf. *Rupicapra*)	1 (0.3%)				
Hemibos cf. *gracilis*	1 (0.3%)	1 (2.4%)	1 (1.5%)	1 (2.7%)	
Hemitragus albus	16 (5.5%)	3 (7.1%)	4 (6.0%)	4 (10.8%)	3 (6.3%)
Praeovibos sp.	1 (0.3%)				
Soergelia minor	20 (6.9%)	1 (2.4%)			
Cervidae indet. (cf. *Capreolus*)	1 (0.3%)				
Metacervocerus rhenanus	33 (11.4%)	6 (14.3%)	4 (6.0%)	5 (11.6%)	8 (16.7%)
Praemegaceros cf. *verticornis*	56 (19.3%)	7 (16.7%)	5 (7.5%)	2 (4.7%)	5 (10.4%)
Hippopotamus antiquus	5 (1.7%)	1 (2.4%)	7 (10.4%)	1 (2.3%)	5 (10.4%)
Equus altidens	91 (31.4%)	10 (23.8%)	5 (7.5%)	14 (32.6%)	3 (6.3%)
Equus sp.		2 (4.8%)	9 (13.4%)	5 (11.6%)	13 (27.1%)
Equus suessenbornensis			2 (3.0%)	2 (4.7%)	2 (4.2%)
Stephanorhinus hundsheimensis	7 (2.4%)	5 (11.9%)	8 (11.9%)	2 (4.7%)	2 (4.2%)
Mammuthus meridionalis	5 (1.7%)	2 (4.8%)	13 (19.4%)	3 (7.0%)	1 (2.1%)
Hystrix sp.	2 (0.7%)	1 * (2.4%)	1 * (1.5%)	1 * (2.3%)	1 (2.1%)
Total	290	42	67	43	48

The Orce sites have provided relevant information on the late Early Pleistocene large mammals that inhabited southern Europe, on their paleocommunities and also on the human groups that inhabited the region (e.g., [34,81–88]). Their richness and uniqueness have allowed us to model and compare the paleoecological conditions that preceded and followed the first hominin arrival in Western Europe [41,42]. Thus, these sites offer unique opportunities for paleoecological analyses. We have conducted several paleoecological studies on the Orce sites, analyzing both CC and TAB [25,41,42,45,65,79,87]. However, we have not yet addressed the comparison of CC and TAB values between VM, BL and FN3. PSEco, with its estimates of survival and mortality profiles, provides optimal scenarios for the large herbivore species, with conditions of stability and stationarity, averaging the temporal fluctuations of their populations [30,54]. Thus, our PSEco proposal can be considered as an ideal situation and thus be used to analyze how the faunal assemblages deviate from the situation represented by this model and why, as we did in a preliminary analysis with the BL and FN3 records [65]. Assuming that the estimates of CC and TAB obtained from PSEco can be considered under optimal ecological conditions, our main objective in this study is to analyze whether the records from these sites can be correlated with the representation that herbivorous mammals had in the paleocommunity and/or with the meat that carnivores and humans could obtain from them and to compare the assemblages of VM with those of BL and FN3. For doing so, we estimate the CC and TAB of the large herbivore community of VM, BL and FN3 and compare them with the relative abundances of species at these sites.

2. Materials and Methods

Based on the materials and methods used in previous analyses, this study aims to reconstruct the paleocommunities of large herbivorous mammals preserved at the Orce sites, focusing on Venta Micena (VM), Barranco León (BL) and Fuente Nueva-3 (FN3) (Table 1), specifically in quarries 3 and 4 of Venta Micena (VM3 and VM4, respectively), the Upper and Lower Archaeological Levels of FN3 (FN3-UAL and FN3-LAL, respectively) and level D of Barranco León (BL-D). These faunal assemblages contain at least 11 species of large herbivores (>10 kg), meeting the criterion of recording at least 8 prey species proposed by Rodríguez-Gómez et al. [43] to identify those Pleistocene faunal assemblages with high conservation completeness. In the analysis of CC and TAB, we used the same species as those of the previous analysis [37,45] and considered FN3 and BL together because they had the same faunal assemblages [22,37,41,45]. In addition to the information derived from the faunal lists, we used Rodríguez-Gómez et al. [45] estimates of prey life history trait values on the basis of their modern analogues (Table 2). We reconstructed their survival and mortality profiles using these values. We used survival profiles to estimate the average body mass of herbivore populations and CC (see [37]). Mortality profiles allowed for the estimation of TAB for the secondary consumers in the paleoecosystems (see [30,40,41,45,55]). The life history traits included are adult and neonate body mass (ABM and NBM, respectively), age at first birth (or age of sexual maturity + pregnancy) (AFB), number of litters per year (LY), litter size (LS) and longevity (L). Estimates of mean adult body mass (ABM) were based on metric measurements from fossil bones and teeth [37] (Table 2).

Table 2. Herbivore life history traits derived from comparison with living analogues data taken from [45]. Abbreviations: ABM (adult body mass, in kg); AFB (age at first birth, in years); LS (litter size); LY (litters per year); NBM (neonate body masses, in kg); L (longevity, in years); D (density, in ind./km^2). Densities were estimated using Damuth's [89] equation (see text).

Order	**Family**	**Species**	**ABM**	**AFB**	**LS**	**LY**	**NBM**	**L**	**D**
Artiodactyla	Bovidae	*Ammotragus europaeus*	135	2.00	1.19	1.00	4.95	19.2	2.38
Artiodactyla	Bovidae	*Bison* sp.	450	2.62	1.00	0.91	25.79	25.0	0.92
Artiodactyla	Bovidae	Bovidae indet. (cf. *Rupicapra*)	25	2.00	1.19	1.00	1.89	19.2	9.03
Artiodactyla	Bovidae	*Hemibos* cf. *gracilis*	300	2.50	1.00	0.96	14.50	22.4	1.27
Artiodactyla	Bovidae	*Hemitragus albus*	75	2.00	1.19	1.00	3.28	19.2	3.79
Artiodactyla	Bovidae	*Praeovibos* sp.	315	2.00	1.19	1.00	9.96	19.2	1.22
Artiodactyla	Bovidae	*Soergelia minor*	225	2.00	1.19	1.00	7.45	19.2	1.59
Artiodactyla	Cervidae	Cervidae indet. (cf. *Capreolus*)	25	2.86	1.00	1.10	1.82	20.8	9.03
Artiodactyla	Cervidae	*Metacervocerus rhenanus*	95	2.86	1.00	1.10	5.57	20.8	3.14
Artiodactyla	Cervidae	*Praemegaceros* cf. *verticornis*	400	2.86	1.00	1.10	18.63	20.8	1.01
Artiodactyla	Hippopotamidae	*Hippopotamus antiquus*	3200	4.00	1.00	0.52	40.20	54.5	0.20
Perissodactyla	Equidae	*Equus altidens*	350	3.50	1.00	0.67	30.70	38.8	1.12
Perissodactyla	Equidae	*Equus suessenbornensis*	565	3.50	1.00	0.67	54.69	38.8	0.77
Perissodactyla	Rhinocerotidae	*Stephanorhinus hundsheimensis*	1000	6.75	1.00	0.36	41.75	47.0	0.49
Proboscidea	Elephantidae	*Mammuthus meridionalis*	6000	11.25	1.13	0.24	101.00	65.0	0.12
Rodentia	Hystricidae	*Hystrix refossa*	20	1.46	1.51	1.51	0.31	20.0	10.77
Rodentia	Hystricidae	*Hystrix* sp.	15	1.46	1.51	1.51	0.31	20.0	13.52

In order to estimate CC or prey biomass of paleocommunities, in this study, we followed the approach of Rodríguez-Gómez et al. [37]. In the case of estimating the amount of TAB provided by the prey community, we applied the PSEco model [45]. Both the estimation of CC by means of survival profiles and the estimation of TAB by means of mortality profiles require values of the average body mass of individuals at different ages and population densities. These approaches take into account the proportion of subadults, an aspect that is relevant for CC estimates (see [37]) or for analyses aimed at estimating the exploitation of meat resources by large predators, since body size is one of the most fundamental parameters in prey selection [74,90–92]. For the estimation of body mass of prey species at distinct age intervals, we followed the proposal of Zullinger et al. [93]:

$$M(t) = ABM * e^{-e^{-K(t-I)}}, \tag{1}$$

where ABM is the asymptotic body mass (that is, the adult body mass in g), M (t) is the mass at age t, K is the growth rate constant (days^{-1}) and I is the age at turning point (days). K refers to the adult body mass according to the equation:

$$log(K) = -0.901 - 0.302 * log(ABM) \tag{2}$$

Mean mass values for each age interval were estimated as the arithmetic mean of the two most extreme values within each age interval. To estimate density values, we used the equation developed by Damuth [89] for European mixed temperate forests:

$$log(D) = -0.79 * log(ABM) + 4.33; r^2 = 0.94 \tag{3}$$

where D is the density of the population (ind./km^2) and ABM is expressed in g.

To estimate CC for the Orce paleocommunities, we used the approach of Rodríguez-Gómez et al. [37], which takes into account the relative proportion of individuals (l_i) and body mass (M_i) in each age interval:

$$B = \sum_{i=1}^{n} l_i * M_i * D,\ i = 1, \ldots, n. \tag{4}$$

l_i was calculated from survival profiles and age structures obtained from the Weibull model [45,53,54]:

$$l_i = \frac{X_i}{\sum_{i=1}^{n} X_i},\ i = 1, \ldots n, \tag{5}$$

with X_i being the number of individuals in each age interval. The biomass that each age interval contributes to the total biomass of the population is derived from the proportion of individuals and body mass per age interval and population density. By adding the biomass of all species, the paleoecosystem CC is calculated.

For TAB, we used PSEco (see [45]), which estimates the number of individuals that could die annually without causing their populations to collapse using mortality profiles of large herbivores of a community (see [30,53,54]). PSEco uses the faunal lists (Table 1), the values of life history traits (Table 2) and the prey species densities in the paleoecosystems to estimate the amount of prey biomass that can be extracted from a paleoecosystem on an annual basis. We used an equation similar to equation 4, substituting l_i for the proportion of deaths between ages (d_i) ($d_x = l_x - l_{x+1}$):

$$Output\ Biomass = \sum_{i=1}^{n} d_i * M_i * D,\ i = 1, \ldots, n. \tag{6}$$

The total output biomass (TBO) is the sum of the biomass output of all species in the community results, as presented by Rodríguez-Gómez et al. [40]. From the TBO, PSEco employs a "wastage factor" that estimates the percentage of biomass that is not used by the secondary consumers (e.g., skin, horns and bones) (see [30,40,44,53,54]). The result is the biomass available for the secondary consumers (in kg/km^2*year^{-1} and kcal/km^2*year^{-1}), which is called TAB (Total Available Biomass) in the PSEco model [45]. Since the Weibull model provides many mortality profiles, PSEco selects only the extreme values corresponding to maximum and minimum subadult mortalities [53,54], where TAB-min is the available biomass corresponding to maximum subadult mortality (and minimum adult mortality) and TAB-MAX refers to the reverse situation.

For both CC and TAB, we divided biomasses into six classes: Class 1: 10–45 kg; Class 2: 45–90 kg; Class 3: 90–180 kg; Class 4: 180–360 kg; Class 5: 360–1000 kg; Class 6: >1000 kg. Thus, we can consider the importance of body size as the most significant parameter in prey selection [74,90–92] as well as the contribution of each population to the different body size classes, which in turn allows to compare values and patterns between CC and TAB.

Based on the results of CC and TAB, we estimated the relative percentage of each family in each index. We grouped the species into families to facilitate and simplify the analyses. For the fossil record, we used the minimal number of individuals (MNI) values to estimate relative percentages (Table 1). We are aware of the tendency of MNIs to underestimate common species and overestimate rare ones when considering the MNI (see [75]). However, this allows us to consider the presence of some species that are represented by scarce fossil or ichnofossil remains in the record. The comparison between the relative proportions of families in the CC, TAB and fossil record was performed using the χ^2 test.

3. Results

Tables 3 and 4 show the values obtained for the Carrying Capacity (CC) and available meat (TAB) provided by the different species of primary consumers of the faunal assemblages of Venta Micena (VM), Barranco León (BL) and Fuente Nueva-3 (FN3). These values are averages of those obtained from the survival and mortality profiles. The CC of Venta Micena was 3813 kg/km^2*year and that of Fuente Nueva-3 and Barranco León was 3535 kg/km^2*year, while the TAB values were 468 and 387 kg/km^2*year, respectively. With these values, CC was 8 and 9 times higher than TAB in these sites, respectively, and the relative percentage of TAB to CC were 12.28% and 10.96%, respectively. These percentages can be interpreted as the annual turnover rates of these faunal sets that could be consumed by the secondary consumers without causing ecosystem degradation. For both VM (Table 3) and FN3/BL (Table 4), the species that contributed the most biomass to the CC was *Mammuthus meridionalis* (534 kg/km^2*year in both cases), while the species that contributed the least biomass to the ecosystems was the porcupine (*Hystrix*) (135 and 138 kg/km^2*year, respectively). The opposite situation occurred with the values of TAB, where the species that provided the most meat to the environment was the porcupine (42 kg/km^2*year) and the one providing the least was the mammoth (18 kg/km^2*year). This is because species with low reproductive rates, such as the megaherbivores, cannot tolerate high rates of mortality, an aspect that species with high reproductive rates, such as the porcupine, can tolerate (see Table 2) [45]. As can be seen in Tables 3 and 4, most species contribute biomass to three size classes for both CC and TAB, with the exception of porcupines, bovidae indet. (cf. *Rupicapra*) and Cervidae indet. (cf. *Capreolus*) from VM, which only contribute to the first class (10–45 kg), and goats *Hemitragus albus* and horses *Equus altidens*, which both contribute to two classes.

Figure 1 shows the estimated CC and TAB values for VM, FN3 and BL distributed across the six size classes provided by PSEco [45]. As mentioned above, we grouped the species values into families to simplify and facilitate comparisons. Differences in biomass distribution patterns can be observed between VM and FN3/BL for both CC and TAB. In terms of CC, two blocks can be distinguished for both VM and FN3/BL, formed by the first three size classes and the last three ones, with the second block standing out in the two assemblages with the highest biomass (Figure 1A,B). The largest differences between the two assemblages are found in class 1 (10–45 kg) and class 4 (180–360 kg), with class 1 in VM contributing more biomass than classes 2 (45–90 kg) and 3 (90–180 kg) and 4 more than 5 (360–1000 kg) and 6 (>1000 kg) (Figure 1A). This is not the case for FN3/BL (Figure 1B). In the case of TAB, classes 1 and 4 are also prominent in VM (Figure 1C). However, the distribution in FN3/BL was more homogeneous, except for class 6, which had a lower value (Figure 1D). Comparing the figures of CC with those of TAB, it is possible to observe the differences in the biomass contribution of megaherbivores to one or the other index, playing a major role in CC and a very secondary one in TAB (Figure 1). The families Bovidae and Cervidae contribute to all size classes except the one in excess of 1000 kg (class 6), where the main contribution is made by the members of the families Hippopotamidae and Elephantidae (Figure 1). Equids in VM are only represented by *E. altidens* and contribute biomass to two size classes. In contrast, two species (*E. altidens* and *E. suessenbornensis*) are present in FN3/BL and contribute to four size classes.

Figures 2 and 3 show the proportions of the different families according to the estimates of CC, TAB and minimum number of individuals (MNI) obtained for each site (Table 1). In VM, bovids and cervids stand out in the estimates of CC, TAB and in the relative abundance of the VM3 and VM4 quarries. In these quarries, equid remains are also relevant, which is not the case for CC and TAB. The χ^2 tests show significant differences between the CC and TAB values with relative abundance in the VM quarries, but no significant differences between the two quarries ($\chi^2 = 11.709$; $p = 0.068795$), supporting the suggestions of Palmqvist et al. [79] that these assemblages have a similar composition. In terms of CC and TAB values, VM3 and VM4 show higher proportions of cervids and equids and lower representations of bovids and porcupines. VM4 shows proportions of rhino *Stephanorhinus hundsheimensis* close to CC and mammoths close to TAB values. Although the χ^2 analysis shows no differences between the proportions of the different families in the VM3 and VM4 assemblages, it can be seen that VM3 has lower proportions of mammoth, rhinoceros and porcupine and higher proportions of bovids than VM4 (Figure 2C,D). If we distribute the proportion of the different species in three body mass categories (small: 10–90 kg; medium-large: 90–600 kg; megaherbivores: >600 kg) (Table 5), we can see that in both VM3 and VM4 there is a greater proportion of medium-to-large species, although in

VM4 megaherbivores reach almost 20% of the assemblage while in VM3 they are 6%. In the case of BL and FN3, bovids and cervids also stand out in the values of CC, TAB and in the fossil record, as recorded by MNI counts, as well as equids in the latter. The χ^2 tests show no significant differences between the CC values and those of the UAL level of FN3 ($\chi^2 = 4.6274$; $p = 0.5924$). Regarding CC and TAB values, FN3-LAL and BL-D show higher estimates for equids and lower values for bovids, porcupines and rhinoceros (Figure 3). FN3-LAL shows cervid values close to CC and rhinoceros close to TAB values and it is noteworthy that the representation of equids is 49%. In the case of BL-D, values close to CC are observed for hippo *Hippopotamus antiquus* and close to TAB for rhinoceros (Figure 3). For both CC and TAB, FN3-UAL has higher values for equids and mammoths, lower values for bovids and porcupines and similar values for cervids and hippos (Figure 3). Regarding the distribution by body size categories (Table 5), very close values can be observed for the CC of the FN3/BL and FN3-UAL records, where the biomass is concentrated in medium-large species (>50%) and megaherbivores (>35%). In FN3-LAL and BL-D, most species are of medium to large size (~75%), with megaherbivores being more relevant in BL-D (17%), while in FN3-LAL both small species and megaherbivores are similarly relevant (12% and 14%, respectively) (Table 5).

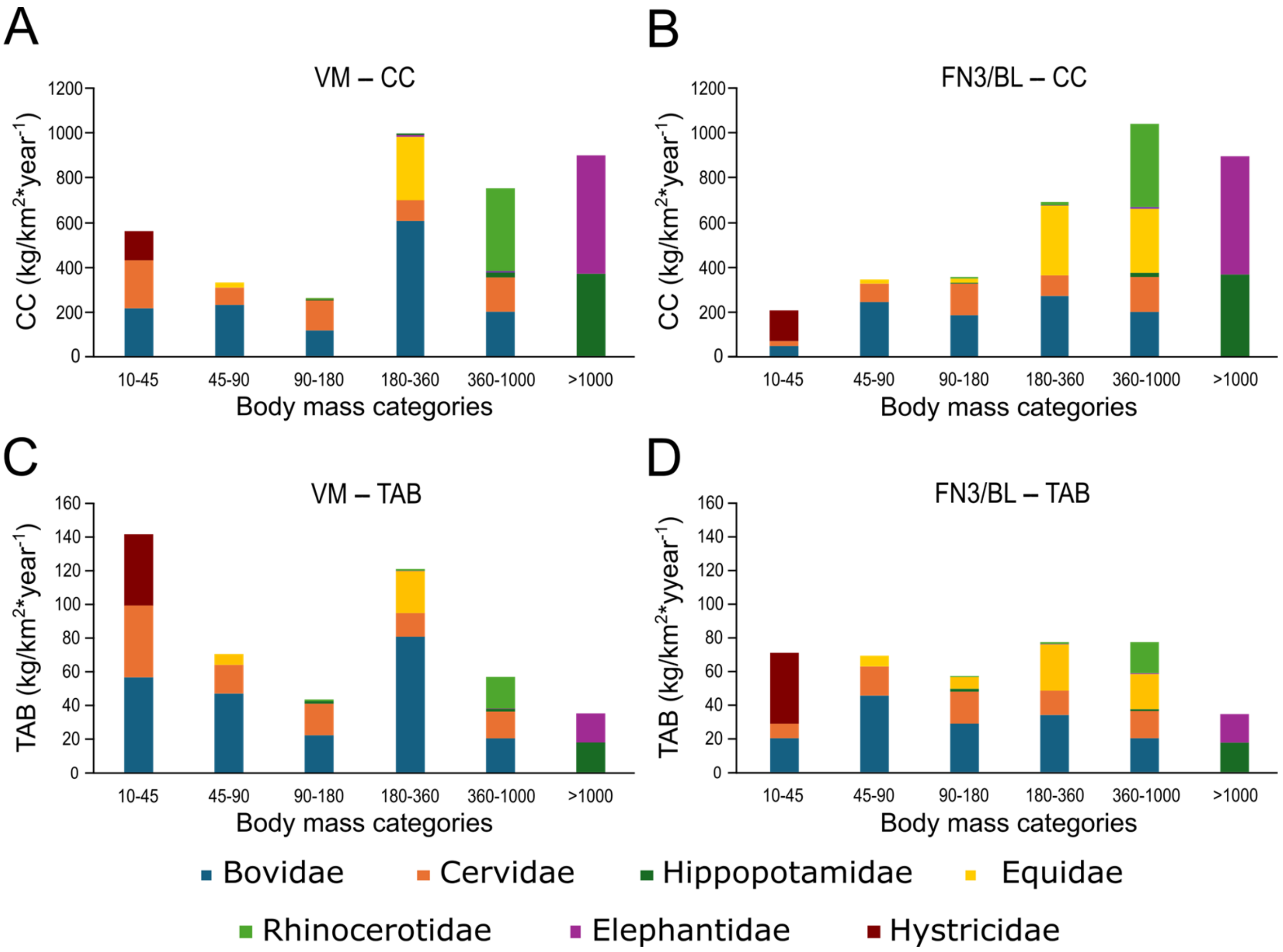

Figure 1. Histograms of Carrying Capacity (CC, in kg/km^2*year^{-1}) for Venta Micena (**A**) and Fuente Nueva-3/Barranco León (**B**) together with the values of Total Available Biomass (TAB, in kg/km^2*year^{-1}) by body mass categories (10–45 kg: Class 1; 45–90 kg: Class 2; 90–180 kg: Class 3; 180–360 kg: Class 4; 360–1000 kg: Class 5; >1000 kg: Class 6) for both paleocommunities ((**C**,**D**), respectively).

Table 3. Estimated values of Carrying Capacity (CC, in kg/km2*year^{-1}) and Total Available Biomass (TAB, in kg/km^2*year^{-1}) from the PSEco model for the Venta Micena (VM) faunal assemblage by body mass classes (Class 1: 10–45 kg; Class 2: 45–90 kg; Class 3: 90–180 kg; Class 4: 180–360 kg; Class 5: 360–1000 kg; Class 6: >1000 kg).

CC	***Bison* sp.**	**Bovidae Indet. (cf. *Rupicapra*)**	***Hemibos* cf. *gracilis***	***Hemitragus albus***	***Praeovibos* sp.**	***Soergelia minor***	**Cervidae Indet. (cf. *Capreolus*)**	***Metacervocerus rhenanus***	***Praemegaceros* cf. *verticornis***	***Hippopotamus antiquus***	***Equus altidens***	***Stephanorhinus hundsheimensis***	***Mammuthus meridionalis***	***Hystrix* sp.**	
Class 1	0.00	178.31	0.00	24.70	0.00	20.00	184.29	22.68	0.00	0.00	0.00	0.00	0.00	135.34	
Class 2	18.85	0.00	18.68	178.51	18.75	0.00	0.00	60.96	18.62	0.00	18.15	0.00	0.00	0.00	
Class 3	0.00	0.00	28.29	0.00	27.79	60.51	0.00	139.91	0.00	4.06	0.00	6.06	0.00	0.00	
Class 4	60.10	0.00	212.66	0.00	186.96	146.18	0.00	0.00	91.17	0.00	287.27	13.21	2.03	0.00	
Class 5	201.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	153.58	21.56	0.00	373.10	4.91	0.00	
Class 6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	368.07	0.00	0.00	526.60	0.00	
Total	280.53	178.31	259.63	203.20	233.50	226.69	184.29	223.55	263.37	393.68	305.42	392.37	533.54	135.34	CC = 3813.42
TAB	***Bison* sp.**	**Bovidae Indet.(cf. *Rupicapra*)**	***Hemibos* cf. *gracilis***	***Hemitragus albus***	***Praeovibos* sp.**	***Soergelia minor***	**Cervidae Indet. (cf. *Capreolus*)**	***Metacervocerus rhenanus***	***Praemegaceros* cf. *verticornis***	***Hippopotamus antiquus***	***Equus altidens***	***Stephanorhinus hundsheimensis***	***Mammuthus meridionalis***	***Hystrix* sp.**	
Class 1	0.00	38.13	0.00	10.26	0.00	8.31	34.19	8.55	0.00	0.00	0.00	0.00	0.00	42.21	
Class 2	4.35	0.00	6.43	28.97	7.31	0.00	0.00	10.39	6.58	0.00	6.52	0.00	0.00	0.00	
Class 3	0.00	0.00	4.92	0.00	5.59	11.76	0.00	18.76	0.00	1.51	0.00	0.94	0.00	0.00	
Class 4	7.99	0.00	26.44	0.00	26.57	19.82	0.00	0.00	14.03	0.00	24.83	1.11	0.21	0.00	
Class 5	20.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.90	1.68	0.00	18.65	0.27	0.00	
Class 6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.60	0.00	0.00	17.03	0.00	
Total	32.74	38.13	37.78	39.24	39.47	39.88	34.19	37.71	36.52	20.79	31.35	20.70	17.50	42.21	TAB = 468.21

Table 4. Estimated values of Carrying Capacity (CC, in kg/km^2*year^{-1}) and Total Available Biomass (TAB, in kg/km^2*year^{-1}) from the PSEco model for the Fuente Nueva-3 (FN3) and Barranco León (BL) faunal assemblages by body mass classes (Class 1: 10%–45 kg; Class 2: 45–90 kg; Class 3: 90–180 kg; Class 4: 180–360 kg; Class 5: 360–1000 kg; Class 6: >1000 kg).

CC	***Ammotragus europaeus***	***Bison* sp.**	***Hemibos* cf. *gracilis***	***Hemitragus albus***	***Metacervocerus rhenanus***	***Praemegaceros* cf. *verticornis***	***Hippopotamus antiquus***	***Equus altidens***	***Equus suessenbornensis***	***Stephanorhinus hundsheimensis***	***Mammuthus meridionalis***	***Hystrix refossa***	
Class 1	23.48	0.00	0.00	24.70	22.68	0.00	0.00	0.00	0.00	0.00	0.00	138.30	
Class 2	30.05	18.85	18.68	178.51	60.96	18.62	0.00	18.15	0.00	0.00	0.00	0.00	
Class 3	157.94	0.00	28.29	0.00	139.91	0.00	4.06	0.00	19.09	6.06	0.00	0.00	
Class 4	0.00	60.10	212.66	0.00	0.00	91.17	0.00	287.27	24.70	13.21	2.03	0.00	
Class 5	0.00	201.58	0.00	0.00	0.00	153.58	21.56	0.00	286.43	373.10	4.91	0.00	
Class 6	0.00	0.00	0.00	0.00	0.00	0.00	368.07	0.00	0.00	0.00	526.60	0.00	
Total	211.46	280.53	259.63	203.20	223.55	263.37	393.68	305.42	330.21	392.37	533.54	138.30	CC = 3535.26
TAB	***Ammotragus europaeus***	***Bison* sp.**	***Hemibos* cf. *gracilis***	***Hemitragus albus***	***Metacervocerus rhenanus***	***Praemegaceros* cf. *verticornis***	***Hippopotamus antiquus***	***Equus altidens***	***Equus suessenbornensis***	***Stephanorhinus hundsheimensis***	***Mammuthus meridionalis***	***Hystrix refossa***	
Class 1	10.44	0.00	0.00	10.26	8.55	0.00	0.00	0.00	0.00	0.00	0.00	41.98	
Class 2	6.19	4.35	6.43	28.97	10.39	6.58	0.00	6.52	0.00	0.00	0.00	0.00	
Class 3	24.37	0.00	4.92	0.00	18.76	0.00	1.51	0.00	6.86	0.94	0.00	0.00	
Class 4	0.00	7.99	26.44	0.00	0.00	14.03	0.00	24.83	2.90	1.11	0.21	0.00	
Class 5	0.00	20.40	0.00	0.00	0.00	15.90	1.68	0.00	20.43	18.65	0.27	0.00	
Class 6	0.00	0.00	0.00	0.00	0.00	0.00	17.60	0.00	0.00	0.00	17.03	0.00	
Total	41.00	32.74	37.78	39.24	37.71	36.52	20.79	31.35	30.19	20.70	17.50	41.98	TAB = 387.49

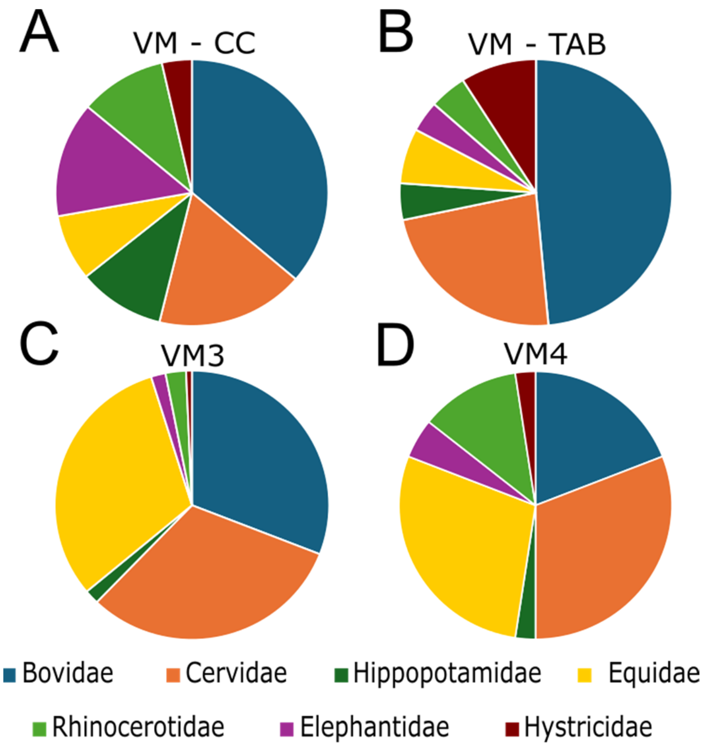

Figure 2. Carrying Capacity (CC) (**A**) and Total Available Biomass (TAB) (**B**) estimated for the Venta Micena (VM) site. The relative abundances of herbivores in the VM3 (**C**) and VM4 (**D**) quarries, estimated from values of minimum number of individuals (MNI) from [78,79], is also shown.

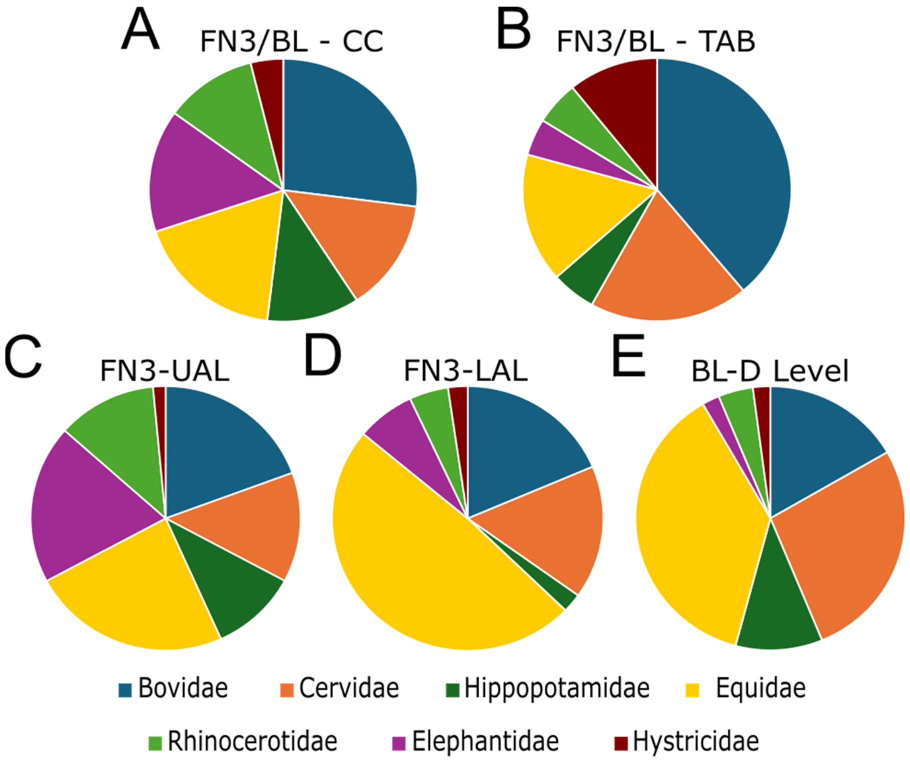

Figure 3. Carrying Capacity (CC) (**A**) and Total Available Biomass (TAB) (**B**) for Fuente Nueva-3 (FN3) and Barranco León (BL). The relative abundance of herbivores in the Upper Archeological Level (UAL-FN3) (**C**) and Lower Archeological Level of FN3 (LAL-FN3) (**D**) and the BL-D Level (**E**), estimated from the minimum number of individuals (MNI) values of [22,68], is depicted.

Table 5. Percentages of species by gross body size classes in the CC and TAB estimates for Venta Micena (VM-CC and VM-TAB, respectively) and Fuente Nueva-3 and Barranco León (FN3/BL-CC and FN3/BL-TAB, respectively) sites, in the fossil record of the Venta Micena 3 (VM3) and Venta Micena 4 (VM4) quarries, in the UAL and LAL levels of Fuente Nueva-3 (FN3–UAL and FN3–LAL, respectively) and in the D level of Barranco León (BL-D). The species were divided into three size categories: small (10–90 kg), medium-large (90–600 kg) and megaherbivores (>600 kg). Species included in the small size class: Bovidae indet. (cf. *Rupicapra*), Cervidae indet. (cf. *Capreolus*), *Hemitragus albus* and *Hystrix* sp. Species included in the medium-large size class: *Ammotragus europaeus*, *Bison* sp., *Hemibos* cf. *gracilis*, *Praeovibos* sp., *Soergelia minor*, *Metacervocerus rhenanus*, *Praemegaceros* cf. *verticornis*, *Equus altidens*, *Equus suessenbornensis* and *Equus* sp. Species included in the megaherbivores size class: *Hippopotamus antiquus*, *Stephanorhinus hundsheimensis* and *Mammuthus meridionalis*.

	Small Size	Medium-Large Size	Megaherbivores
VM-CC	18	47	35
VM-TAB	33	55	13
VM3	7	87	6
VM4	10	71	19
FN3/BL-CC	10	53	37
FN3/BL-TAB	21	64	15
FN3–UAL	7	51	42
FN3–LAL	12	74	14
BL-D Level	8	75	17

4. Discussion

As used in studies of ecology and paleoecology, Carrying Capacity (CC) represents the optimal and ideal conditions of a population and/or community, being the maximum growth it could have in the long term (see [33]). As previously proposed by Palmqvist et al. [65], in this study, we used these optimal conditions to evaluate and interpret the fossil assemblages, especially in communities rich enough to be considered as completely preserved in the fossil record. To estimate these optimal conditions, we used the PSEco model, which provided values of CC and Total Available Biomass or meat (TAB), as well as the ecological densities of carnivores and humans that could sustain the ecosystems [45]. For those paleocommunities of large mammals from Orce and the Sierra de Atapuerca, PSEco produced results for predator–prey biomass ratios comparable to those found in modern African ecosystems [45], which are close to steady conditions [31]. These results validated our approach as a means to estimate these ecological indices (i.e., CC and TAB).

The CC results indicate similar values for the VM and FN3/BL faunal assemblages, although VM (3813 kg/km^2*year) would have a slightly higher value than FN3/BL (3535 kg/km^2*year) (Tables 3 and 4), as we advocated in various previous studies ([37,42,45,94]; however, see [95]). These values are similar to those presented by Nairobi National Park (Kenya), Serengeti National Park (Tanzania), the Savuti area of Chobe National Park (Botswana) and Kruger National Park (South Africa), including for megaherbivores [31]. In terms of TAB, there are greater differences between VM and FN3/BL, with VM being more productive than FN3/BL due to the composition of the prey species and their differences in reproductive rates (see [41,42,45,54]). When the distribution patterns of CC and TAB are analyzed, there emerge differences between both communities (Figure 1). Following Ripple and Van Valkenburgh [96], Rodríguez-Gómez et al. [43] suggested that the differences between VM and FN3/BL in the patterns of TAB distribution among size classes could be due to top-down forces, because the body size classes with higher values of TAB (45–90, 180–360, 360–1000 kg) correspond to those of the preferred prey of the three top predators of FN3/BL (wild dog *Lycaon lycaonoides* as well as saber-tooths *Homotherium latidens* and *Megantereon whitei*) [71]. As shown in Figure 1D, the distribution of TAB is similar in classes 1 (10–45 kg), 2 (45–90 kg), 4 (180–360 kg) and 5 (360–1000 kg). The pattern of TAB distribution between size classes in VM shows more inequality between these classes than in FN3/BL, with classes 1 and 4 standing out (Figure 1C). This situation could have led to a greater competition for meat in VM, as more biomass was concentrated in specific size classes, rather than being more homogeneously distributed among the size classes (Figure 1C), as shown in FN3/BL (Figure 1D). This concentration of resources could favor the specialist carnivores, while the homogeneous distribution could favor the generalist ones, who could exploit a wider spectrum of resources. The compositional differences in the guild of secondary consumers between VM and FN3/BL are mainly due to the presence of the European jaguar *Panthera* cf. *gombaszoegensis* in VM and of *Homo* sp. in FN3/BL, since the jaguar was a specialist flesh-eating hypercarnivore and humans were an omnivorous and more generalist species that probably behaved more as a scavenger than as a predator. In this way, this dietary difference could support our proposal. However, in a previous study, Rodríguez-Gómez et al. [42] argued that competition was lower in VM than in FN3/BL due to the greater TAB of VM. Therefore, they did not relate the presence of humans in FN3 and BL to the presence of greater amounts of resources compared to VM, a site that does not preserve any evidence of the presence of humans [97], but rather to climatic or biogeographic barriers to hominin dispersal that posed a delay on the settlement of Western Europe until about 1.4 Ma (i.e., the age estimated for FN3/BL) [88]. Nevertheless, it is possible that conditions in FN3 and BL favored human presence due to a more homogeneous distribution of resources among size classes. This suggestion would argue against the proposal that the distribution of TAB in FN3/BL was driven by top-down forces. It will be interesting to further investigate this line of work in future studies to reach a conclusion.

Using our CC and TAB results as a reference for the analysis of the fossil record from Orce, it is observed that VM3 and VM4 are very different from the expected values (Figure 2). The giant hyenas, the biological agents involved in the formation of these assemblages, mainly focused on medium and large-sized species (between 90 and 600 kg) (Table 5), while small-sized species and megaherbivores were less relevant for them. This is more pronounced in VM3 than in VM4, where megaherbivores make up 6% of the total, while in VM4 they reach 19%. Nevertheless, according to our analysis, VM3 and VM4 do not show significant differences in the family composition of their assemblages (Figure 2C,D). This supports the suggestion of Palmqvist et al. [79] that there are no differences in the bone accumulation and modification patterns of the agent involved in these accumulations, *P. brevirostris*, only in the length of time that the skeletal remains were exposed to hyena consumption and weathering before the assemblage was capped by sedimentation of micritic limestone. The differences observed in VM3 and VM4 with respect to the expected values according to CC and TAB may be due to the coincidence of the activity of different carnivores in the selection and consumption of prey, since *P. brevirostris* scavenged the prey hunted selectively by saber-toothed predators (*Homotherium latidens* and *Megantereon whitei*) and wild dogs (*Lycaon lycaonoides*), being a strict scavenger of solitary habits as opposed to the present spotted hyena, which acts more like an active hunter [76,86,98].

Significant differences with the expected values of CC and TAB are observed for BL-D. However, it is interesting to note that no significant differences are observed between BL-D and the VM quarries, VM3 (χ^2 = 11.403; p = 0.0767) and VM4 (χ^2 = 12.215; p = 0.0573). Based on these results, we could argue that the factors involved in site formation for VM, together with the conservation biases involved in the accumulation of bone remains at this site [76], may have been similar to those involved in forming BL-D. It should be noted, however, that there is evidence of the presence of humans at BL-D [22,62,63,66]. The limited characteristics of the stone tools from FN3 and BL, including the small size of the flint and limestone flakes, have led to the assumption that access to large and megaherbivore prey through hunting would have been difficult for these hominins [65,86], which led researchers to consider that the optimal strategy of these humans at BL would be that of a strict and generalist scavenger [41]. It is most likely that these hominins played a role similar to that of *P. brevirostris* at VM, although the hyena was better equipped for aggressive scavenging (i.e., kleptoparasitism). Table 5 shows that the presence of megaherbivores in BL-D (17%, with hippos at 10%) is similar to that of VM4 (19%) and also to that expected in FN3/BL (15%) according to the TAB values, but is somewhat further from the TAB value derived for VM (13%). This suggests that the available meat resources of megaherbivores were exploited, but that the small-sized species were exploited less intensively than expected (Table 5). Depending on body size, carnivorous species are limited in the exploitation of certain resources [90], with larger carnivores having the ability and need to exploit larger prey [99]. Thus, these results appear to be consistent with the proposed *Megantereon*-hominin-*Pachycrocuta* model for FN3 (see discussions in [65,68]), which proposes that humans had secondary acquisition of prey remains from saber-tooths and other top predators. Saber-tooth cats would kill prey and consume only a part of the carcass (i.e., the softer tissues), leaving a large amount of meat and all the nutrients in the bones intact for scavenging by humans and, subsequently, by the giant hyenas. Saber-tooths would not focus on small prey; rather, they would take advantage of the meat resources available in the young megaherbivores, but their preferred prey would be medium and large ungulates (90–600 kg), as deduced by Palmqvist et al. [34,84,85] based on isotopic analyses of fossil bone collagen in VM3.

A similar case to that of BL-D can be observed for FN3-LAL, with very close values of medium-to-large species and megaherbivores (Table 5), with the relative percentages of megaherbivores very close to those provided by the TAB estimates (Figure 3 and Table 5). However, FN3-LAL shows significant differences with the other assemblages analyzed in the proportion represented by the different families, with equids showing a high representation (Figure 3D). In terms of prey size, FN3-LAL has a greater presence of small-sized species than the other fossil assemblages analyzed (Table 5). On the other hand, horses are an animal resource used by humans throughout the Pleistocene and Assaf [100] has recently argued that horses were an essential resource for Early Pleistocene humans due to the nutritional value of their meat, especially bone marrow, which is superior to that of other ungulates (see [100] and references therein). Given the importance of human presence at this level of FN3, as indicated by the finding of abundant manuports (i.e., limestone cobbles used by the hominins for breaking bones and accessing the medullary cavities; see [22,64]), both the greater number of small-sized species and horses may be a reflection of higher activity of humans in the FN3-LAL compared to other levels.

Regarding FN3-UAL, this is the only faunal assemblage that does not show significant differences with the expected value of CC, with a high value of megaherbivores (42%) as well as medium and large species (51%) and a low abundance of small species (7%) (Table 5). In comparison with the FN3-LAL level, Espigares et al. [64] and Palmqvist et al. [101] have suggested that this level is a death trap associated with quicksand due to its geological composition (two-thirds of layer 5 of LAL are fine and very fine sands and the remaining third is composed of silts and clays, which were combined with the oligosaline waters of the Orce paleolake). The functioning of this level as a quicksand trap for herbivores is consistent with the fact that no significant differences are observed with the values expected by CC (Figure 3A,D). As can be seen in Figure 3, FN3-UAL gives slightly higher values than expected for mammoths and rhinos in the CC scenario, which could be explained by the high weight per unit area supported by their legs, which posed a risk of entrapment ([101], see Figure 8). These results support that this methodology may allow the interpretation of sites that functioned as traps for the fauna recorded. This would be expected if these traps showed no relevant bias, trapping the species according to their abundance in the ecosystems, which is what CC measures. The only exception would be the largest species, like elephants, which are scarce in the ecosystem but tend to be overrepresented in the natural traps given the elevated weight supported by their feet, which results in a greater risk of entrapment. It will be interesting to confirm these results by applying the methodology to other sites with conditions similar to those of the UAL level of FN3.

Given the usefulness that CC values can have in evaluating sites that originally functioned as traps, could TAB be useful in evaluating the faunal composition of some sites? Our TAB results have allowed us to discuss megaherbivore values at BL-D and their consistency with the subsistence strategies of humans and the giant hyenas, as well as deviations from equid values at FN3-LAL. For this part, it is an interesting index to make interpretative proposals on the sites, but it is a more complex index to analyze than CC, because it is difficult to find similar and compatible scenarios for FN3-LAL, as that in the case of the traps considered for CC. Primarily, predators select prey based on body size [74,90–92], so large carnivores must prey on large prey species for reasons of energy efficiency [99]. Thus, sites where large felids played a relevant role, such as the Orce sites, do not show a high abundance of small prey because they were not frequently preyed upon by these predators. In present-day African ecosystems, lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) prey on different species, most of which weigh less than 600 kg [102,103] and their prey selection overlaps significantly [104]. In Kruger National Park, for example, spotted hyenas prey primarily on wildebeest (*Connochaetes taurinus*, 163 kg), buffalo (*Syncerus caffer*, 520 kg), Burchell's zebra (*Equus quagga burchellii*, 220 kg), greater kudu (*Tragelaphus strepsiceros*, 170 kg) and impala (*Aepyceros melampus*, 44 kg) [105] and for lions, buffalo, wildebeest and zebra, with a distinction between males and females, with males preferring buffalo and females wildebeest and zebra [106]. According to the CC values of Hatton et al. [31], buffalo, zebra and wildebeest account for approximately 30% of the total prey biomass or 67% if megaherbivores are not considered. In the case of Kalahari (South Africa), the main prey for lions and hyenas is the gemsbok (*Oryx gazella*, 162 kg), with small prey such as springbok (*Antidorcas marsupialis*, 32 kg) or porcupines (*Hystrix*, <20 kg) also taken in the absence of large ungulates [107–111]. CC estimates for the Kalahari are very low at 258 kg/km^2*year [31], with these species accounting for >75% of CC. In Serengeti National Park (Tanzania), spotted hyenas hunt mainly wildebeest, Thomson's gazelle (*Eudorcas thomsonii*, 18 kg) and zebra [112–114] and seven species account for 90% of the total meat intake of lions: buffalo, kongoni (*Alcelaphus buselaphus*, 125 kg), Thomson's gazelle (*Gazella thomsonii*, 18 kg), topi (*Damaliscus lunatus*, 108 kg), warthog (*Phacochoerus aethiopicus*, 55 kg), wildebeest and zebra [115]. In Serengeti National Park, total CC is approximately 2875 kg/km^2*year and 2158 kg/km^2*year excluding megafauna, with these species accounting for 82% of the CC [31]. Spotted hyenas have a preferred prey range of 56 to 182 kg, with the mode at 102 kg (Hayward 2006). This range may be slightly higher for lions, with wildebeest being the preferred prey in parts of South Africa and East Africa [27]. Nevertheless, both spotted hyenas and lions may prey on young individuals of megafauna, such as elephants, giraffes, hippopotamuses and rhinoceroses [116,117], but Hayward [104] argued that hyenas tend to avoid buffalo, plains zebras and giraffes. Given the above, we can generally expect hyenas and lions to hunt prey between 50 and 200 kg, which tend to be the most abundant, with megaherbivores being a less exploited resource, as well as species under 50 kg, except in poor resource conditions, as in the Kalahari [31,107–111]. Therefore, if we focus on the prey consumed by spotted hyenas and lions, we will have a very biased view of the resources that could be exploited from the ecosystem and, in turn, many difficulties in relating them to TAB values. This could be overcome by combining different carnivore species with different preferred prey sizes (e.g., leopard, cheetah, wild dog, etc.), which could provide a ratio of prey remains that would approach the values of meat available in the ecosystems. However, it would be very difficult to find an accumulation of remains of different predators preserved at the same site and that the prey species are represented according to resource availability. For this reason, this approach makes it difficult to obtain relative values for fossil sites similar to those based on TAB values. Another possibility could be provided by generalist species that could exploit all the resources of the environment with a similar preference for all potential prey, both as scavengers and as dominant predators of the ecosystem. It will be interesting to evaluate sites where humans exerted a major role in the paleoecosystem after the inception of the Acheulean (i.e., mode 2) techno-culture, being the main accumulating agent, in order to interpret their ability to exploit the resources of the ecosystems in which they lived.

5. Conclusions

Knowing the ecological conditions under which humans evolved during the Pleistocene is of great interest in the study of human evolution, and indices such as Carrying Capacity (CC) and Total Available Biomass (TAB) are useful to infer aspects of these conditions in the paleoecosystems. These indices represent optimal conditions for the communities studied and therefore serve as a reference for the evaluation and interpretation of faunal assemblages. Our results lead us to propose that (i) the distribution of TAB in FN3/BL could have been more beneficial for humans than in VM being a species with a generalist behavior; (ii) the differences observed between the fossil assemblages and CC and TAB values are due to the intervention of different secondary consumers; (iii) humans may have been more important in shaping the faunal assemblage of FN3-LAL than in the one of BL-D because the former shows a higher abundance of small herbivores and equids, both of which were essential resources for humans in the Early Pleistocene; and (iv) the relative abundances of taxa from FN3-UAL show consistency with the interpretation that this level acted as a quicksand trap, showing a proportion of taxa similar to those present in the ecosystem under CC conditions, with a slightly higher abundance of rhinoceroses and mammoths than expected. Considering all of the above, it can be argued that the approach of this work, using CC and TAB values to evaluate the fossil faunal assemblages, is useful with its application in sites rich in fauna such as those of Orce. It will be interesting to use this methodology and working perspective in other sites to test its usefulness and sites considered natural traps could be an ideal next step.

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Abbreviations

BL-D	Barranco León-Level D
CC	Carrying Capacity
FN3-LAL	Fuente Nueva 3-Lower Archaeologial Level
FN3-UAL	Fuente Nueva 3-Upper Archaeological Level
MNI	minimum number of individuals
PSEco	Paleosynecological model

TAB	Total Available Biomass
VM3	Venta Micena quarry 3
VM4	Venta Micena quarry 4

References

1. Ferraro, J.V.; Plummer, T.W.; Pobiner, B.L.; Oliver, J.S.; Bishop, L.C.; Braun, D.R.; Ditchfield, P.W.; Seaman, J.W., III; Binetti, K.M.; Seaman, J.W., Jr.; et al. Earliest Archaeological Evidence of Persistent Hominin Carnivory. *PLoS ONE* **2013**, *8*, e62174. [CrossRef] [PubMed]
2. Speth, J.D. Early Hominid Subsistence Strategies in Seasonal Habitats. *J. Archaeol. Sci.* **1987**, *14*, 13–29. [CrossRef]
3. Roebroeks, W. Hominid behaviour and the earliest occupation of Europe: An exploration. *J. Hum. Evol.* **2001**, *41*, 437–461. [CrossRef] [PubMed]
4. Hublin, J.J.; Richards, M.P. *The Evolution of Hominin Diets. Integrating Approaches to the Study of Palaeolithic Subsistence*; Spinger: Leipzig, Germany, 2009; p. 288.
5. El Zaatari, S.; Grine, F.E.; Ungar, P.S.; Hublin, J.J. Ecogeographic variation in Neandertal dietary habits: Evidence from occlusal molar microwear texture analysis. *J. Hum. Evol.* **2011**, *61*, 411–424. [CrossRef] [PubMed]
6. Henry, A.G.; Brooks, A.G.; Piperno, D.R. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 486–491. [CrossRef]
7. Hardy, K.; Buckley, S.; Collins, M.J.; Estalrrich, A.; Brothwell, D.; Copeland, L.; García-Tabernero, A.; García-Vargas, S.; De La Rasilla, M.; Lalueza-Fox, C.; et al. Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. *Naturwissenschaften* **2012**, *99*, 617–626. [CrossRef]
8. Sistiaga, A.; Mallol, C.; Galván, B.; Summons, R.E. The Neanderthal Meal: A New Perspective Using Faecal Biomarkers. *PLoS ONE* **2014**, *9*, e101045. [CrossRef]
9. Estalrrich, A.; El Zaatari, S.; Rosas, A. Dietary reconstruction of the El Sidrón Neandertal familial group (Spain) in the context of other Neandertal and modern hunter-gatherer groups. A molar microwear texture analysis. *J. Hum. Evol.* **2017**, *104*, 13–22. [CrossRef]
10. Power, R.C.; Salazar-García, D.C.; Rubini, M.; Darlas, A.; Harvati, K.; Walker, M.; Hublin, J.J.; Henry, A.G. Dental calculus indicates widespread plant use within the stable Neanderthal dietary niche. *J. Hum. Evol.* **2018**, *119*, 27–41. [CrossRef]
11. Salazar-García, D.C.; Power, R.C.; Rudaya, N.; Kolobova, K.; Markin, S.; Krivoshapkin, A.; Henry, A.G.; Richards, M.P.; Viola, B. Dietary evidence from Central Asian Neanderthals: A combined isotope and plant microremains approach at Chagyrskaya Cave (Altai, Russia). *J. Hum. Evol.* **2021**, *156*, 102985. [CrossRef]
12. Cordain, L.; Miller, J.B.; Eaton, S.B.; Mann, N.; Holt, S.H.; Speth, J.D. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. *Am. J. Clin. Nutr.* **2000**, *71*, 682–692. [CrossRef]
13. Marlowe, F.W. Hunter-Gatherers and Human Evolution. *Evol. Anthropol.* **2005**, *14*, 54–67. [CrossRef]
14. Fiorenza, L.; Benazzi, S.; Estalrrich, A.; Kullmer, O. Diet and cultural diversity in Neanderthals and modern humans from dental macrowear analyses. In *Dental Wear in Evolutionary and Biocultural Contexts*; Academic Press: Cambridge, MA, USA, 2020; pp. 39–72. [CrossRef]
15. Binford, L.R. *Constructing Frames of Reference. An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Sets*, 1st ed.; University of California Press: Berkeley, CA, USA, 2001; p. 624.
16. Gaudzinski, S.; Roebroeks, W. Adults only. Reindeer hunting at the Middle Palaeolithic site Salzgitter Lebenstedt, Northern Germany. *J. Hum. Evol.* **2000**, *38*, 497–521. [CrossRef]
17. Bocherens, H.; Drucker, D.G.; Billiou, D.; Patou-Mathis, M.; Vandermeersch, B. Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: Review and use of a multi-source mixing model. *J. Hum. Evol.* **2005**, *49*, 71–87. [CrossRef] [PubMed]
18. Richards, M.P.; Trinkaus, E. Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 16034–16039. [CrossRef] [PubMed]
19. Saladié, P.; Huguet, R.; Díez, C.; Rodríguez-Hidalgo, A.; Cáceres, I.; Vallverdú, J.; Rosell, J.; Bermúdez de Castro, J.M.; Carbonell, E. Carcass transport decisions in *Homo antecessor* subsistence strategies. *J. Hum. Evol.* **2011**, *61*, 425–446. [CrossRef]
20. Speth, J.D. *The Paleoanthropology and Archaeology of Big-Game Hunting*; Springer: Berlin/Heidelberg, Germany, 2010; p. 268.
21. Smith, G.M. Neanderthal megafaunal exploitation in Western Europe and its dietary implications: A contextual reassessment of La Cotte de St Brelade (Jersey). *J. Hum. Evol.* **2015**, *78*, 181–201. [CrossRef]
22. Espigares, M.P.; Palmqvist, P.; Guerra-Merchán, A.; Ros-Montoya, S.; García-Aguilar, J.M.; Rodríguez-Gómez, G.; Serrano, F.J.; Martínez-Navarro, B. The earliest cut marks of Europe: A discussion on hominin subsistence patterns in the Orce sites (Baza basin, SE Spain). *Sci. Rep.* **2019**, *9*, 15408. [CrossRef]
23. Kahlke, R.D.; Gaudzinski, S. The blessing of a great flood: Differentiation of mortality patterns in the large mammal record of the Lower Pleistocene fluvial site of Untermassfeld (Germany) and its relevance for the interpretation of faunal assemblages from archaeological sites. *J. Archaeol. Sci.* **2005**, *32*, 1202–1222. [CrossRef]
24. Stringer, C.B.; Finlayson, J.C.; Barton, R.N.E.; Fernández-Jalvo, Y.; Cáceres, I.; Sabin, R.C.; Rhodes, E.J.; Currant, A.P.; Rodríguez-Vidal, J.; Giles-Pacheco, F.; et al. Neanderthal exploitation of marine mammals in Gibraltar. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 14319–14324. [CrossRef]

25. Palmqvist, P.; Rodríguez-Gómez, G.; Figueirido, B.; García-Aguilar, J.M.; Pérez-Claros, J.A. On the ecological scenario of the first hominin dispersal out of Africa. *L'anthropologie* **2022**, *126*, 102998. [CrossRef]
26. Coe, M.J.; Cumming, D.H.; Phillipson, J. Biomass and Production of Large African Herbivores in Relation to Rainfall and Primary Production. *Oecologia* **1976**, *22*, 341–354. [CrossRef]
27. Schaller, G.B. *The Serengeti Lion: A Study of Predator-Prey Relations*; The University of Chicago Press: Chicago, IL, USA; London, UK, 1972; p. 518.
28. Owen-Smith, N. *Megaherbivores: The Influence of Very Large Body Size on Ecology*; Cambridge University Press: Cambridge, UK, 1988; p. 382.
29. Hayward, M.W.; O'Brien, J.; Kerley, G.I.H. Carrying capacity of large African predators: Predictions and tests. *Biol. Conserv.* **2007**, *139*, 219–229. [CrossRef]
30. Rodríguez-Gómez, G.; Rodríguez, J.; Martín-González, J.A.; Goikoetxea, I.; Mateos, A. Modeling trophic resource availability for the first human settlers of Europe: The case of Atapuerca TD6. *J. Hum. Evol.* **2013**, *64*, 645–657. [CrossRef]
31. Hatton, I.A.; McCann, K.S.; Fryxell, J.M.; Davies, T.J.; Smerlak, M.; Sinclair, A.R.E.; Loreau, M. The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. *Science* **2015**, *349*, aac6284-1. [CrossRef] [PubMed]
32. Rodríguez, J.; Blain, H.-A.; Mateos, A.; Martín-González, J.A.; Cuenca-Bescós, G.; Rodríguez-Gómez, G. Ungulate carrying capacity in Pleistocene Mediterranean ecosystems: Evidence from the Atapuerca sites. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2014**, *393*, 122–134. [CrossRef]
33. Sayre, N.F. The Genesis, History, and Limits of Carrying Capacity. *Ann. Am. Assoc. Geogr.* **2008**, *98*, 120–134. [CrossRef]
34. Palmqvist, P.; Gröcke, D.R.; Arribas, A.; Fariña, R.A. Paleoecological reconstruction of a lower Pleistocene large mammal community using biogeochemical (δ^{13}C, δ^{15}N, δ^{18}0, Sr: Zn) and ecomorphological approaches. *Paleobiology* **2003**, *29*, 205–229. [CrossRef]
35. Barnosky, A.D. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 11543–11548. [CrossRef]
36. Rodríguez, J.; Mateos, A. Carrying capacity, carnivoran richness and hominin survival in Europe. *J. Hum. Evol.* **2018**, *118*, 72–88. [CrossRef]
37. Rodríguez-Gómez, G.; Palmqvist, P.; Martínez-Navarro, B.; Martín-González, J.A.; Bermúdez de Castro, J.M. Mean body size estimation in large mammals and the computation of biomass in past ecosystems: An application to the Pleistocene sites of Orce and Sierra de Atapuerca (Spain). *C. R. Palevol.* **2022**, *21*, 207–233. [CrossRef]
38. Vidal-Cordasco, M.; Ocio, D.; Hicker, T.; Marín-Arroyo, A.B. Ecosystem productivity affected the spatiotemporal disappearance of Neanderthals in Iberia. *Nat. Ecol. Evol.* **2022**, *6*, 1644–1657. [CrossRef] [PubMed]
39. Vidal-Cordasco, M.; Terlato, G.; Ocio, D.; Marín-Arroyo, A. Neanderthal coexistence with *Homo sapiens* in Europe was affected by herbivore carrying capacity. *Sci. Adv.* **2023**, *9*, eadi4099. [CrossRef] [PubMed]
40. Rodríguez-Gómez, G.; Mateos, A.; Martín-González, J.A.; Blasco, R.; Rosell, J.; Rodríguez, J. Discontinuity of Human Presence at Atapuerca during the Early Middle Pleistocene: A Matter of Ecological Competition? *PLoS ONE* **2014**, *9*, e101938. [CrossRef]
41. Rodríguez-Gómez, G.; Palmqvist, P.; Rodríguez, J.; Mateos, A.; Martín-González, J.A.; Espigares, M.P.; Ros-Montoya, S.; Martínez-Navarro, B. On the ecological context of the earliest human settlements in Europe: Resource availability and competition intensity in the carnivore guild of Barranco Leon-D and Fuente Nueva-3 (Orce, Baza Basin, SE Spain). *Quat. Sci. Rev.* **2016**, *143*, 69–83. [CrossRef]
42. Rodríguez-Gómez, G.; Palmqvist, P.; Ros-Montoya, S.; Espigares, M.P. Resource availability and competition intensity in the carnivore guild of the Early Pleistocene site of Venta Micena (Orce, Baza Basin, SE Spain). *Quat. Sci. Rev.* **2017**, *164*, 154–167. [CrossRef]
43. Rodríguez-Gómez, G.; Rodríguez, J.; Martín-González, J.A.; Mateos, A. Evaluating the impact of *Homo*-carnivore competition in European human settlements during the early to middle Pleistocene. *Quat. Res.* **2017**, *88*, 129–151. [CrossRef]
44. Rodríguez-Gómez, G.; Cassini, G.H.; Palmqvist, P.; Bargo, M.S.; Toledo, N.; Martín-González, J.A.; Muñoz, N.A.; Kay, R.F.; Vizcaíno, S.F. Testing the hypothesis of an impoverished predator guild in the Early Miocene ecosystems of Patagonia: An analysis of meat availability and competition intensity among carnivores. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2020**, *554*, 109805. [CrossRef]
45. Rodríguez-Gómez, G.; Martín-González, J.A.; Espigares, M.P.; Bermúdez de Castro, J.M.; Martínez-Navarro, B.; Arsuaga, J.L.; Palmqvist, P. From meat availability to hominin and carnivore biomass: A paleosynecological approach to reconstructing predator-prey biomass ratios in the Pleistocene. *Quat. Sci. Rev.* **2024**, *328*, 108474. [CrossRef]
46. Bermúdez de Castro, J.M.; Díez Fernández-Lomana, J.C.; Mosquera Martínez, M.; Nicolás Checa, M.E.; Pérez Pérez, A.; Rodríguez Méndez, J.; Sánchez Marco, A. El nicho ecológico de los homínidos del Pleistoceno Medio de Atapuerca. *Complutum* **1995**, *6*, 9–56.
47. Fariña, R.A. Trophic relationships among Lujanian mammals. *Evol. Theory* **1996**, *11*, 125–134.
48. Vizcaíno, S.F.; Fariña, R.A.; Zárate, M.A.; Bargo, M.S.; Schultz, P. Palaeoecological implications of the mid-Pliocene faunal turnover in the Pampean Region (Argentina). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2004**, *213*, 101–113. [CrossRef]
49. Vizcaíno, S.F.; Bargo, M.S.; Kay, R.F.; Fariña, R.A.; Di Giacomo, M.; Perry, J.M.G.; Prevosti, F.J.; Toledo, N.; Cassini, G.H.; Fernicola, J.C. A baseline paleoecological study for the Santa Cruz Formation (late–early Miocene) at the Atlantic coast of Patagonia, Argentina. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2010**, *292*, 507–519. [CrossRef]

50. Marín Arroyo, A.B. *Arqueozoología en el Cantábrico Oriental Durante la Transición Pleistoceno/Holoceno*; Editorial Universidad de Cantabria, Colección Difunde: Santander, Spain, 2010; p. 686.
51. Meloro, C.; Clauss, M. Predator-prey biomass fluctuations in the Plio-Pleistocene. *Palaios* **2012**, *27*, 90–96. [CrossRef]
52. Palombo, M.R. To what extent could functional diversity be a useful tool in inferring ecosystem responses to past climate changes? *Quat. Int.* **2016**, *413 Pt B*, 15–31. [CrossRef]
53. Martín-González, J.A.; Mateos, A.; Rodríguez-Gómez, G.; Rodríguez, J. A parametrical model to describe a stable and stationary age structure for fossil populations. *Quat. Int.* **2016**, *413*, 69–77. [CrossRef]
54. Martín-González, J.A.; Rodríguez-Gómez, G.; Palmqvist, P. Survival profiles from linear models versus Weibull models: Estimating stable and stationary population structures for Pleistocene large mammals. *J. Archaeol. Sci. Rep.* **2019**, *25*, 370–386. [CrossRef]
55. Rodríguez-Gómez, G.; Pérez-Fernández, E.; Fernández, P.; Arsuaga, J.L.; Díez, C.; Arceredillo, D. Palaeoecology of the Southern chamois from Valdegoba Cave (Burgos, Spain) and its exploitation by the Neanderthals. *Lethaia* **2022**, *55*, 1–25. [CrossRef]
56. Wilson, O.E.; Parker, A.K. Low predator competition indicates occupation of macro-predatory niches by giant Miocene reptiles at La Venta, Colombia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2023**, *632*, 111843. [CrossRef]
57. Pérez-Pérez, A.; Bravo-Cuevas, V.M.; Fernández, P. Population dynamics of *Equus conversidens* (Perissodactyla, Equidae) from the late Pleistocene of Hidalgo (central Mexico): Comparison with extant and fossil equid populations. *J. South Am. Earth Sci.* **2021**, *106*, 103100. [CrossRef]
58. Moullé, P.E.; Echassoux, A.; Martínez-Navarro, B. *Ammotragus europaeus*: Une nouvelle espèce de Caprini (Bovidae, Mammalia) du Pléistocène inférieur à la grotte du Vallonnet (France). *C. R. Palevol* **2004**, *3*, 663–673. [CrossRef]
59. Martínez-Navarro, B.; Palmqvist, P.; Madurell, J.; Ros-Montoya, S.; Espigares, M.P.; Torregrosa, V.; Pérez-Claros, J.A. La Fauna de Grandes mamíferos de Fuente Nueva-3 y Barranco León-5: Estado de la Cuestión. In *Ocupaciones Humanas en el Pleistoceno Inferior y Medio de la Cuenca de Guadix-Baza*; Toro, I., Martínez-Navarro, B., Agustí, J., Eds.; Junta de Andalucía, Consejería de Cultura, Arqueología Monografías: Sevilla, Spain, 2010; pp. 197–236.
60. Madurell-Malapeira, J.; Martínez-Navarro, B.; Ros-Montoya, S.; Espigares, M.P.; Toro, I.; Palmqvist, P. The earliest European badger (*Meles meles*), from the Late Villafranchian site of Fuente Nueva 3 (Orce, Granada, SE Iberian Peninsula). *C. R. Palevol* **2011**, *10*, 609–615. [CrossRef]
61. Ros-Montoya, S.; Bartolini-Lucenti, S.; Espigares, M.P.; Palmqvist, P.; Martínez- Navarro, B. First review of lyncodontini material (Mustelidae, Carnivora, Mammalia) from the lower Pleistocene archaeo-palaeontological sites of Orce (southeastern Spain). *Riv. Ital. Paleontol. Stratigr.* **2021**, *127*, 33–47. [CrossRef]
62. Barsky, D.; Celiberti, V.; Cauche, D.; Grégire, S.; Levègue, F.; de Lumley, H.; Toro-Moyano, I. Raw material discernment and technological aspects of the Barranco León and Fuente Nueva 3 stone assemblages (Orce southern Spain). *Quart. Int.* **2010**, *223–224*, 201–219. [CrossRef]
63. Barsky, D.; Vergès, J.-M.; Sala, R.; Menéndez, L.; Toro-Moyano, I. Limestone percussion tools from the late Early Pleistocene sites of Barranco León and Fuente Nueva 3 (Orce, Spain). *Phil. Trans. R. Soc. B* **2015**, *370*, 20140352. [CrossRef]
64. Espigares, M.P.; Palmqvist, P.; Rodríguez-Ruiz, M.D.; Ros-Montoya, S.; Pérez-Ramos, A.; Rodríguez-Gómez, G.; Guerra-Merchán, A.; García-Aguilar, J.M.; Granados, A.; Campaña, I.; et al. Sharing food with hyenas: A latrine of *Pachycrocuta brevirostris* in the Early Pleistocene assemblage of Fuente Nueva-3 (Orce, Baza Basin, SE Spain). *Archaeol. Anthropol. Sci.* **2023**, *15*, 81. [CrossRef]
65. Palmqvist, P.; Rodríguez-Gómez, G.; Martínez-Navarro, B.; Espigares, M.P.; Figueirido, B.; Ros-Montoya, S.; Guerra-Merchán, A.; Granados, A.; García-Aguilar, J.M.; Pérez-Claros, J.A. Déjà vu: On the use of meat resources by sabretooths, hominins, and hyaenas in the Early Pleistocene site of Fuente Nueva 3 (Guadix-Baza Depression, SE Spain). *Archaeol. Anthropol. Sci.* **2023**, *15*, 17. [CrossRef]
66. Toro-Moyano, I.; Martínez-Navarro, B.; Agustí, J.; Souday, C.; Bermúdez de Castro, J.M.; Martinón-Torres, M.; Fajardo, B.; Duval, M.; Falguères, C.; Oms, O.; et al. The oldest human fossil in Europe, from Orce (Spain). *J. Hum. Evol.* **2013**, *65*, 1–9. [CrossRef]
67. Titton, S.; Oms, O.; Barsky, D.; Bargalló, A.; Serrano-Ramos, A.; García-Solano, J.; Sánchez-Bandera, C.; Yravedra, J.; Blain, H.-A.; Toro-Moyano, I.; et al. Oldowan stone knapping and percussive activities on a raw material reservoir deposit 1.4 million years ago at Barranco León (Orce, Spain). *Archaeol. Anthropol. Sci.* **2021**, *13*, 108. [CrossRef]
68. Yravedra, J.; Solano, J.A.; Courtenay, L.A.; Saarinen, J.; Linares-Matás, G.; Luzón, C.; Serrano-Ramos, A.; Herranz-Rodrigo, D.; Cámara, J.M.; Ruiz, A.; et al. Use of meat resources in the Early Pleistocene assemblages from Fuente Nueva 3 (Orce, Granada, Spain). *Archaeol. Anthropol. Sci.* **2021**, *13*, 213. [CrossRef]
69. Duval, M.; Falguères, C.; Bahain, J.-J.; Grün, R.; Shao, Q.; Aubert, M.; Dolo, J.-M.; Agusti, J.; Martínez-Navarro, B.; Palmqvist, P.; et al. On the limits of using combined U-series/ESR method to date fossil teeth from two Early Pleistocene archaeological sites of the Orce area (Guadix-Baza basin, Spain). *Quat. Res.* **2012**, *77*, 481–482. [CrossRef]
70. Álvarez, C.; Parés, J.M.; Granger, D.; Duval, M.; Sala, R.; Toro, I. New magnetostratigraphic and numerical age of the Fuente Nueva-3 site (Guadix-Baza Basin, Spain). *Quat. Int.* **2015**, *389*, 224–234. [CrossRef]
71. Arribas, A.; Palmqvist, P. The first human dispersal to Europe: Remarks on the archaeological and palaeoanthropological record from Orce (Guadix-Baza basin, southeastern Spain). *J. Hum. Evol.* **2002**, *17*, 55–78. [CrossRef]
72. Turq, A.; Martínez-Navarro, B.; Palmqvist, P.; Arribas, A.; Agustí, J.; Rodríguez-Vidal, J. Le Plio-Pléistocène de la région d'Orce, province de Grenada, Espagne: Bilan et perspectivas de Recherche. *Paléo* **1996**, *8*, 161–204. [CrossRef]

73. Martínez-Navarro, B.; Turq, A.; Agustí, J.; Oms, O. Fuente Nueva-3 (Orce, Granada, Spain) and the first human occupation of Europe. *J. Hum. Evol.* **1997**, *33*, 611–620. [CrossRef] [PubMed]
74. Palmqvist, P.; Martínez-Navarro, B.; Arribas, A. Prey selection by terrestrial carnivores in a Lower Pleistocene paleocommunity. *Paleobiology* **1996**, *22*, 514–534. [CrossRef]
75. Arribas, A.; Palmqvist, P. Taphonomy and palaeoecology of an assemblage of large mammals: Hyaenid activity in the lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). *Geobios* **1998**, *31*, 3–4. [CrossRef]
76. Palmqvist, P.; Arribas, A. Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals. *Paleobiology* **2001**, *27*, 512–530. [CrossRef]
77. Granados, A.; Oms, O.; Anadón, P.; Ibáñez-Insa, J.; Kaakinen, A.; Jiménez-Arenas, J.M. Geochemical and sedimentary constraints on the formation of the Venta Micena Early Pleistocene site (Guadix-Baza basin, Spain). *Sci. Rep.* **2021**, *11*, 22437. [CrossRef]
78. Luzón, C.; Yravedra, J.; Courtenay, L.A.; Saarinen, J.; Blain, H.-A.; DeMiguel, D.; Viranta, S.; Azanza, B.; Rodríguez-Alba, J.J.; Herranz-Rodrigo, D.; et al. Taphonomic and spatial analyses from the Early Pleistocene site of Venta Micena 4 (Orce, Guadix-Baza Basin, southern Spain). *Sci. Rep.* **2021**, *11*, 13977. [CrossRef]
79. Palmqvist, P.; Espigares, M.P.; Pérez-Claros, J.A.; Figueirido, B.; Guerra-Merchán, A.; Ros-Montoya, S.; Rodríguez-Gómez, G.; García-Aguilar, J.M.; Granados, A.; Martínez-Navarro, B. Déjà vu: A reappraisal of the taphonomy of quarry VM4 of the Early Pleistocene site of Venta Micena (Baza Basin, SE Spain). *Sci. Rep.* **2022**, *12*, 705. [CrossRef]
80. Espigares Ortiz, M.P. Análisis y Modelización del Contexto Sedimentario y los Atributos Tafonómicos de los Yacimientos Pleistocénicos del Borde Nororiental de la Cuenca de Guadix-Baza. Ph.D. Thesis, Departamento de Estratigrafía y Paleontología, Universidad de Granada, Granada, Spain, 2010.
81. Martínez-Navarro, B.; Palmqvist, P. Presence of the African Machairodont *Megantereon whitei* (Broom, 1937) (Felidae, carnivora, Mammalia) in the Lower Pleistocene site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. *J. Archaeol. Sci.* **1995**, *22*, 569–582. [CrossRef]
82. Turner, A.; Antón, M. The giant hyaena, *Pachycrocuta brevirostris* (Mammalia, Carnivora, Hyaenidae). *Geobios* **1996**, *29*, 455–468. [CrossRef]
83. Palmqvist, P.; Arribas, A.; Martínez Navarro, B. Ecomorphological study of large canids from the lower Pleistocene of southern Spain. *Lethaia* **1999**, *32*, 75–88. [CrossRef]
84. Palmqvist, P.; Pérez-Claros, J.A.; Janis, C.M.; Figueirido, B.; Torregrosa, V.; Gröcke, D.R. Biogeochemical and ecomorphological inferences on prey selection and resource partitioning among mammalian carnivores in an Early Pleistocene community. *Palaios* **2008**, *23*, 724–737. [CrossRef]
85. Palmqvist, P.; Pérez-Claros, J.A.; Janis, C.M.; Gröcke, D.R. Tracing the ecophysiology of ungulates and predator–prey relationships in an early Pleistocene large mammal community. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2008**, *266*, 95–111. [CrossRef]
86. Palmqvist, P.; Martínez-Navarro, B.; Pérez-Claros, J.A.; Torregrosa, V.; Figueirido, B.; Jiménez-Arenas, J.M.; Espigares, M.P.; Ros-Montoya, S.; de Renzi, M. The giant hyena *Pachycrocuta brevirostris*: Modelling the bone-cracking behavior of an extinct carnivore. *Quat. Int.* **2011**, *243*, 61–79. [CrossRef]
87. Palmqvist, P.; Rodríguez-Gómez, G.; Bermúdez de Castro, J.M.; García-Aguilar, J.M.; Espigares, M.P.; Figueirido, B.; Ros-Montoya, S.; Granados, A.; Serrano, F.J.; Martínez-Navarro, B.; et al. Insights on the Early Pleistocene Hominin Population of the Guadix-Baza Depression (SE Spain) and a Review on the Ecology of the First Peopling of Europe. *Front. Ecol. Evol.* **2022**, *10*, 881651. [CrossRef]
88. Martínez-Navarro, B.; Madurell-Malapeira, J.; Ros-Montoya, S.; Espigares, M.P.; Medin, T.; Hortolà, P.; Palmqvist, P. The Epivillafranchian and the arrival of pigs into Europe. *Quat. Int.* **2015**, *389*, 131–138. [CrossRef]
89. Damuth, J. Population density and body size in mammals. *Nature* **1981**, *290*, 699–700. [CrossRef]
90. Carbone, C.; Mace, G.M.; Roberts, S.C.; Macdonald, D.W. Energetic constraints on the diet of terrestrial carnivores. *Nature* **1999**, *402*, 286–288. [CrossRef] [PubMed]
91. Radloff, F.G.T.; Toit, J.T.D. Large predators and their prey in a southern African savanna: A predator's size determines its prey size range. *J. Anim. Ecol.* **2004**, *73*, 410–423. [CrossRef]
92. Ercoli, M.D.; Prevosti, F.J.; Forasiepi, A.M. The structure of the mammalian predator guild in the Santa Cruz Formation (Late Early Miocene). *J. Mamm. Evol.* **2014**, *21*, 369–381. [CrossRef]
93. Zullinger, E.M.; Ricklefs, R.E.; Redford, K.H.; Mace, G.M. Fitting sigmoidal equations to mammalian growth curves. *J. Mammal.* **1984**, *65*, 607–636. [CrossRef]
94. Palmqvist, P.; Rodríguez-Gómez, G.; Espigares, M.P. Climate and environmental conditions in the Guadix-Baza Depression during the first hominin dispersal in Western Europe: Comment on Saarinen et al. (2021). *Quat. Sci. Rev.* **2022**, *297*, 107731. [CrossRef]
95. Saarinen, J.; Oksanen, O.; Žliobaitė, I.; Fortelius, M.; DeMiguel, D.; Azanza, B.; Bocherens, H.; Luzón, C.; Solano-García, J.; Yravedra, J.; et al. Pliocene to Middle Pleistocene climate history in the Guadix-Baza Basin, and the environmental conditions of early *Homo* dispersal in Europe. *Quat. Sci. Rev.* **2021**, *268*, 107132. [CrossRef]
96. Ripple, W.J.; Van Valkenburgh, B. Linking top-down forces to the Pleistocene megafaunal extinctions. *BioScience* **2010**, *60*, 516–526. [CrossRef]
97. Martínez-Navarro, B. The skull of Orce: Parietal bones or frontal bones? *J. Hum. Evol.* **2002**, *42*, 265–270. [CrossRef]

98. Coca-Ortega, C.; Pérez-Claros, J.A. Characterizing ecomorphological patterns in hyenids: A multivariate approach using postcanine dentition. *PeerJ* **2019**, *6*, e6238. [CrossRef]
99. Carbone, C.; Teacher, A.; Rowcliffe, J.M. The costs of carnivory. *PLoS Biol.* **2007**, *5*, 363–368. [CrossRef]
100. Assaf, E. Set in Stone: Human–Horse Relations as Embodied in Shaped Stone Balls. *Archaeologies* **2024**, *20*, 64–105. [CrossRef]
101. Palmqvist, P.; Campaña, I.; Granados, A.; Martínez-Navarro, B.; Pérez-Ramos, A.; Rodríguez-Gómez, G.; Guerra-Merchán, A.; Ros-Montoya, S.; Rodríguez-Ruiz, M.D.; García-Aguilar, J.M.; et al. The late Early Pleistocene site of Fuente Nueva-3 (Guadix-Baza Depression, SE Spain): A hyena latrine developed on a quicksand trap for megaherbivores? *J. Iber. Geol.* **2024**, 1–27. [CrossRef]
102. Mills, G.; Hofer, H. *Hyaenas. Status Survey and Conservation Action*; IUCN/SSC Hyaena Specialist Group: Gland, Switzerland; IUCN; Cambridge, UK, 1998; 154p.
103. Haas, S.K.; Hayssen, V.; Krausman, P.R. Panthera leo. Mamm. *Species* **2005**, *762*, 1–11. [CrossRef]
104. Hayward, M.W. Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *J. Zool.* **2006**, *270*, 606–614. [CrossRef]
105. Henschel, J.R.; Skinner, J.D. The diet of spotted hyaenas' *Crocuta crocuta* in Kruger National Park. *Afr. J. Ecol.* **1990**, *28*, 69–82. [CrossRef]
106. Funston, P.J.; Mills, G.L.; Biggs, H.C.; Richardson, P.R.K. Hunting by male lions: Ecological influences and socioecological implications. *Anim. Behav.* **1998**, *56*, 1333–1345. [CrossRef] [PubMed]
107. Mills, M.G.L. Prey selection and feeding habits of the large carnivores in the Southern Kalahari. *Koedoe* **1984**, *27*, 281–294. [CrossRef]
108. Mills, M.G.L. *Kalahari Hyaenas: The Comparative Behavioural Ecology of Two Species*; Allen and Unwin Hyman: London, UK, 1990; p. 304.
109. Eloff, F.C. Lion predation in the Kalahari Gemsbok National Park. *J. South Afr. Wildl. Mgmt. Ass.* **1973**, *3*, 59–64.
110. Eloff, F.C. Food ecology of the Kalahari lion *Panthera leo vernayi*. *Koedoe* **1984**, *27*, 249–258. [CrossRef]
111. Turner, A.; Antón, M. *The Big Cats and Their Fossil Relatives*; Columbia University Press: New York, NY, USA, 1997; p. 233.
112. Kruuk, H. *The Spotted Hyena. A Study of Predation and Social Behavior*; The University of Chicago Press: Chicago, IL, USA, 1972; p. 335.
113. Hofer, H.; East, M.L. The commuting system of Serengeti spotted hyaenas: How a predator copes with migratory prey. I. Social organization. *Anim. Behav.* **1993**, *46*, 547–557. [CrossRef]
114. Hofer, H.; East, M.L. Population dynamics, population size, and the commuting system of Serengeti spotted hyaenas. In *Serengeti II: Dynamics, Conservation and Management of an Ecosystem*; Sinclair, A.R.E., Arcese, P., Eds.; University of Chicago Press: Chicago, IL, USA, 1995; pp. 332–363.
115. Scheel, D.; Packer, C. Variation in predation by lions: Tracking a movable feast. In *Serengeti II: Dynamics, Conservation and Management of an Ecosystem*; Sinclair, A.R.E., Arcese, P., Eds.; University of Chicago Press: Chicago, IL, USA, 1995; pp. 299–314.
116. Pienaar, U.D.V.; Riche, E.; Roux, C.S. The use of drugs in the management and control of large carnivorous mammals. *Koedoe* **1969**, *12*, 177–183. [CrossRef]
117. Stander, P.E. The ecology of lions and conflict with people in north-eastern Namibia. Proceedings of a Symposium on Lions and Leopards as Game Ranch Animals, Onderstepoort, South Africa, 24–25 October 1997; van Heerden, J., Ed.; Wildlife Group of the South African Veterinary Association: Onderstepoort, South Africa, 1997; pp. 10–17.