On the ecological context of the earliest human settlements in Europe: Resource availability and competition intensity in the carnivore guild of Barranco León-D and Fuente Nueva-3 (Orce, Baza Basin, SE Spain)

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ABSTRACT

With an age of ~1.4 Ma, the Early Pleistocene archaeopaleontological sites of Barranco León and Fuente Nueva-3 (Orce, Baza Basin, SE Spain) provide the oldest evidence on human presence in Western Europe, including the finding of a deciduous tooth of Homo sp., huge lithic assemblages of Oldowan tradition and abundant cut-marks on large mammal bones. Here we use a mathematical approach based on Leslie matrices to quantify for the large mammal species preserved at the sites the biomass of primary consumers available, the distribution of meat resources among the secondary consumers and the competition intensity within the carnivore guild. The results obtained show a community of large mammals with a high diversity of secondary consumers that would satisfy slightly less than half of their dietary requirements under optimal ecological conditions. In the case of Homo sp., and considering that flesh resources were obtained through the scavenging of ungulate carcasses, the model indicates that the ecosystems of the basin could hold 10–14 individuals per 100 km² during a year, a value that is close to the mean population density of recent hunter-gatherers. These density estimates decrease slightly when a mixed hunting-scavenging strategy is considered and even more in the case of a strict hunting behavior. In addition, the value of the species competition index obtained for Homo sp. is among the lowest of the carnivore guild. These results suggest that the hominin populations that inhabited Southeast Spain during the Early Pleistocene behaved more as opportunistic scavengers than as active predators.

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1. Introduction

During the last decades, increasing evidence indicates that the genus Homo dispersed out of Africa during the late Early Pleistocene (Calabrian, Late Villafranchian). However, a number of issues related to this dispersal event are still subject to debate and controversy, including the chronology of the first human settlements in Western Europe, the dispersal route(s), the technocultural developments of this early human population, the continuity of the initial peopling of Europe, and the ecological context and climatic conditions in which the dispersal event took place (Dennell and Roebroeks, 1996, 2005; Arribas and Palmqvist, 1999; Carbonell et al., 1999, 2008, 2010; Bar-Yosef and Belfer-Cohen, 2001; Dennell, 2003; Antón and Swisher, 2004; Martínez-Navarro, 2004, 2010; Rook et al., 2004; Nikitas and Nikita, 2005; Palombo and Mussi, 2006; Agustí et al., 2009; Moncel, 2010; Palombo,
In this paper, our main goal is to test the availability of animal resources for the hominin populations that inhabited the Baza Basin (SE Spain; García-Aguilar and Palmqvist, 2011) during the late Early Pleistocene, which remains and evidence of anthropic activity have been documented in two archaeopaleontological sites of this sedimentary basin that are located in the vicinity of the town of Orce, Barranco León (BL-D) (Espigares, 2010; Toro-Moyano et al., 2013) and Fuente Nueva-3 (FN-3) (Espigares et al., 2013) (Fig. 1).

The age of these sites has been estimated by biostratigraphy and using the combined U-series/ESR dating method in 1.43 ± 0.38 Ma for BL-D and in 1.19 ± 0.21 Ma for FN-3, respectively (Duval et al., 2012; Toro-Moyano et al., 2013), and there is also a recent age estimate of 1.50 ± 0.31 Ma for FN-3 derived from cosmogenic nuclides (Alvarez et al., 2015). Given these age estimates and according also to biostratigraphic considerations (e.g., Sus ex. gr. scrofa, which marks the beginning of the Epivillafranchian biochron, is first recorded at level TE9 of Atapuerca Sima del Elefante, dated by cosmogenic nuclides to 1.22 ± 0.16 Ma, but is absent from both BL-D and FN-3; Martínez-Navarro et al., 2015), the Late Villafranchian sites of Orce preserve the oldest evidence of human presence in Western Europe (see reviews in Martínez-Navarro et al., 1997, 2014; Arribas and Palmqvist, 1999, 2002; Palmqvist et al., 2005, 2014, 2016; Jiménez-Arenas et al., 2011b; Espigares et al., 2013; Toro-Moyano et al., 2013).

The evidence of human presence from these sites includes the finding of a human deciduous, lower first molar tooth at BL-D (Toro-Moyano et al., 2013) and huge lithic assemblages of Oldowan (i.e., Mode 1) tradition at both localities that include flint flakes, cores and limestone percussion tools (Palmqvist et al., 2005; Toro-Moyano et al., 2009, 2011; Barsky et al., 2015) as well as abundant cut-marks on large mammal bones (Espigares et al., 2013; Toro-Moyano et al., 2013). In fact, taphonomic analysis of the faunal assemblage unearthed from FN-3 has provided evidence...
of intense competition between hominins and hyenas for scavenging an elephant carcass, which is dismembered and surrounded in the sediment by flint flakes and coprolites (Espigares et al., 2013). In addition, the ecological interactions in the large mammals community of the Early Pleistocene of SE Spain have been addressed in Venta Micena (VM), a nearby site dated by biostratigraphy to ~1.6–1.5 Ma that is somewhat older than BL-D and FN-3, using a dual approach based on biogeochemistry (i.e., carbon- and nitrogen isotope values) and ecomorphology (Palmqvist et al., 2003, 2008a, 2008b). These studies have provided interesting clues on the dietary/habitat preferences of the ungulate taxa preserved at VM and also inferences on the predator-prey relationships in the paleocommunity. However, in spite of some controversial remains that were attributed to the genus Homo in the past, it must be noted that no conclusive evidence of human presence at the VM site has been detected by the moment (see reviews in Martínez-Navarro, 2002, 2013; Palmqvist et al., 2005; Espigares, 2010; Jiménez-Arenas et al., 2011b). For this reason, little is known on the patterns of resource partitioning and competitive displacement among the members of the carnivore guild in the ecosystems inhabited by the hominins that first dispersed in Western Europe during Early Pleistocene times and, more specifically, on how these patterns affected the human populations detected in BL-D and FN-3.

With this in mind, we estimated for the large mammal species preserved at BL-D and FN-3 the biomass of primary consumers available and the distribution of meat resources among the secondary consumers. This approach was based on the mathematical model of Rodríguez-Gómez et al. (2013), which allowed quantifying the resources that could have been consumed by the human population that inhabited the ecosystems of BL-D and FN-3. The model has been used by Rodríguez-Gómez et al. (2013) for analyzing the faunal assemblage of level TD6-2 from the Gran Dolina site of Sierra de Atapuerca (NW Spain), which has an age of ~0.9 Ma (Parés et al., 2013). The results obtained in this study suggested the existence of a rich environment, abundant in trophic resources for the hominin population that lived at Atapuerca during late Early Pleistocene times. Here we test if these conditions prevailed also in the surroundings of the paleolake that existed in the Baza Basin during the Late Villafranchian, as recent studies have evidenced for this period of time a contribution of hydrothermal waters linked to tectonic activity in the basin that resulted in a very productive environment (García-Aguilar et al., 2014, 2015).

2. Material and methods

2.1. The faunal assemblages of BL-D and FN-3

The fossil assemblages from BL-D and FN-3 record the same species of large mammals (Table 1), although there are differences in their abundance between both sites: for example, hippo teeth and bones are particularly well-represented in BL-D (Palmqvist et al., 2005; Espigares, 2010), while elephant remains are more abundantly preserved in FN-3 (Ros-Montoya, 2010; Espigares et al., 2013) (for an in-depth discussion of patterns of faunal abundance in the Early Pleistocene sites of Europe, see Madurell-Malapeira et al., 2015). The faunal list of these sites was obtained from Palmqvist et al. (2005), Martínez-Navarro et al. (2010), Espigares et al. (2013), Toro-Moyano et al. (2013), Boscaïni et al. (2015) and Medin et al. (2015), and their taphonomic context was analyzed by Espigares (2010). This analysis was restricted to those mammal species weighing >10 kg, because they include the ungulate species that contribute the main sources of meat and fat for a heterogatherer population, as well as their main potential competitors and/or predators (Binford, 1981, 1985; Gaudzinski and Roebroeks, 2000; Marean, 1989; Owen-Smith and Mills, 2008; Roebroeks, 2001; Speth, 2010). This size interval includes also a number of small-to-medium-sized predators (e.g., the lynx and the painted dog) that may prey on small ungulates that are potentially important in a human diet.

Ten species of primary consumers with body masses ranging between 75 and 6000 kg have been identified in BL-D and FN-3 (Table 1): one proboscidean (Mammutthus meridionalis), three perrissodactyls (Equus altidens, Equus suessenbornensis and Stephanorhinus hundsheimensis) and six artiodactyls (one hippo: Hippopotamus antiquus; three bovids: Bison sp., Hemitragus cf. albus and Ammotragus europaeus; and two cervids: Praemegaceros verticornis and Metacervus rhenanus).

Eight species of secondary consumers, which distribute over a wide size range (12–300 kg), were identified in the faunal assemblage (Table 1): two canids (Canis mosbachensis and Lycaon lycaonoides), three felids (Homotherium latidens, Megantereon whitei and Lynx cf. pardinus), one hyaenid (Pachycrocuta brevirostris) and one primate (Homo sp.). Of these species, the bear shows craniodental morphology indicative of an omnivorous behavior (Palmqvist et al., 2008b; Medin et al., 2015) and its diet was assumed to include only 10% meat based on data from extinction and modern populations of the European brown bear (Ursus arctos) (Parde and Camarra, 1992; Bocherens et al., 2004). In the case of Homo sp., the finding of huge Oldowan tool assemblages in BL-D and FN-3, abundant cut marks on ungulate bones and a close spatial association of flakes with a partial skeleton of elephant in FN-3 (Espigares et al., 2013; Toro-Moyano et al., 2013; Martínez-Navarro et al., 2014) indicates that this early human population was a significant component of the carnivore guild that scavenged the carcasses of large mammals. Among the hypercarnivores (i.e., species whose diet consists exclusively of flesh), the two sabertoothed cats (Homotherium latidens and Megantereon whitei) and the pack-hunting canid (Lycaon lycaonoides) were considered as obligate predators, a behavior unequivocally deduced from them from ecomorphology and isotopic biogeochemistry (Palmqvist et al., 1999, 2002, 2003, 2007, 2008a, 2008b). In contrast, the giant, short-faced hyena (Pachycrocuta brevirostris) was considered as a scavenger, as deduced from taphonomic analysis in VM as well as from skull biomechanics and ecomorphology of the postcrancial skeleton of this bone-cracking hyena, which showed massive limbs with shortened distal bones and a heavy, powerfully built mandible. Finally, a number of small-sized carnivores preserved in the sites (e.g., Vulpes cf. praeglacialis, Pannonictis sp., and Meles meles) were excluded from the analyses because they presumably had a hypo-carnivorous diet, with a consumption of flesh basically derived from small vertebrates (Rodríguez-Gómez et al., 2013).

In the case of Homo sp., a major debate has been focused since the first studies of early hominin sites from Africa on its characterization as a “hunter” or as a “scavenger”. During the 1980s and 1990s, most researchers (for reviews and references, see Espigares et al., 2013) considered that early humans had only access to ungulate carcasses through passive scavenging. However, a number of experimental studies (e.g., Bunn and Ezzo, 1993; Domínguez-
Rodrigo, 1999; Domínguez-Rodrigo and Barba, 2006; Bunn and Pickering, 2010) suggested the possibility that hominins had primary access to these resources. The reason is that although large felids do not consume bone marrow contents (thus opening the opportunity for early humans to scavenge them), they exploit intensively the body of their prey and, consequently, the flesh available in the abandoned carcasses uses to be very scarce. This contradicts the interpretation of the finding of abundant cut marks related to defleshing activities in a number of sites as an evidence of secondary access to ungulate carcasses by the hominins. Instead, the new interpretive context implies that these cut marks would reflect a primary access to ungulate carcasses, with carcass acquisition resulting from hunting, from power scavenging (i.e., kleptoparasitism), or from active searching (see reviews in Domínguez-Rodrigo et al., 2013, 2014). However, the experimental studies cited above were performed on leopards and lions, while most felid specimens from the Orce sites are ascribed to two machairodontine (i.e., saber-toothed) cats, H. latidens and M. whitei. These extinct predators have no modern analogues, but their specialized craniodental anatomy suggests that they were probably less able to exploit their prey than the living pantherine cats. This would result in greater amounts of flesh abandoned in the carcasses of their prey, which would in turn be available for passive scavengers such as the hominins and hyenas (Palmqvist et al., 2007, 2011). Such interpretation makes sense if we consider in this study a scavenging behavior for Homo sp. considering a hunting strategy for these resources (see chapters in Damuth and MacFadden, 1990) when new data were available for BL-D and/or FN-3.

2.2. Methodology applied

The access to animal resources (i.e., meat and fat) by each of the secondary consumers of the Early Pleistocene community of BL-D and FN-3, including the human population, probably depended on: (1) the abundance of animal resources (i.e., population density and demographic structure of ungulate species); (2) the ability of each predator to obtain and process these resources (i.e., differences in hunting success between ambushers in forest and coursers in open plains, or in carcass processing between flesh-eating and bone-cracking carnivores); and (3) the level of competition intensity among the members of the carnivore guild (i.e., competitive displacement and kleptoparasitism).

As noted before, the distribution of meat resources among the secondary consumers of the paleocommunity was analyzed using the mathematical model of Rodríguez-Gómez et al. (2013, 2014), which takes into account their predatory abilities and the competition for these resources. This model estimates also the biomass of primary consumers available to the secondary consumers, which is designed as the “Total Available Biomass” (TAB), and the requirements of the secondary consumers in ideal conditions (i.e., when all secondary consumers fulfill their requirements and reach their maximum population densities), which are designed as the “Total Demanded Biomass” (TDB) (Fig. 2B). For doing so, the model determines the age structure that makes the population of each primary consumer stable, its distribution among body size categories and the average biomass that can be extracted from this population in the long term. In a second step, the distribution of ungulate resources among the secondary consumers is modeled when all secondary consumers fulfill their requirements and reach their maximum population densities, which are designed as the “Total Demanded Biomass” (TDB) (Fig. 2B). For doing so, the model determines the age structure that makes the population of each primary consumer stable, its distribution among body size categories and the average biomass that can be extracted from this population in the long term.

### Table 1

Faunal list and body masses estimated for the large mammals species identified in the fossil assemblages of Barranco León-D (BL-D) and Fuente Nueva-3 (FN-3). The list of species is identical for both sites. The mass value for Homo sp. is the average of the estimates provided by Jiménez-Armas et al. (2014: Suppl. Table) for early Homo (i.e., H. habilis/rudolfensis, H. ergaster and H. erectus).

<table>
<thead>
<tr>
<th>Trophic level, family/subfamily</th>
<th>Species</th>
<th>Body mass (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary consumers</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elephantidae</td>
<td>Mammutthus meridianalis</td>
<td>6000</td>
</tr>
<tr>
<td>Rhinocerotidae</td>
<td>Stephanorhinus hendrikshimensis</td>
<td>1000</td>
</tr>
<tr>
<td>Equidae</td>
<td>Equus altidens</td>
<td>350</td>
</tr>
<tr>
<td>Equidae</td>
<td>Equus suesennbornensis</td>
<td>565</td>
</tr>
<tr>
<td>Hippopotamidae</td>
<td>Hippopotamus antiquus</td>
<td>3200</td>
</tr>
<tr>
<td>Bovinae</td>
<td>Biva sp.</td>
<td>450</td>
</tr>
<tr>
<td>Caprinae</td>
<td>Ammotragus europaeus</td>
<td>135</td>
</tr>
<tr>
<td>Caprinae</td>
<td>Hemitragus cf. albus</td>
<td>75</td>
</tr>
<tr>
<td>Cervidae</td>
<td>Metacervocerus rhenuus</td>
<td>95</td>
</tr>
<tr>
<td>Cervidae</td>
<td>Praemegaceros verticornis</td>
<td>385</td>
</tr>
<tr>
<td>Secondary consumers</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ursidae</td>
<td>Ursus etruscus</td>
<td>300</td>
</tr>
<tr>
<td>Canidae</td>
<td>Canis mosbachensis</td>
<td>12</td>
</tr>
<tr>
<td>Canidae</td>
<td>Lycaon lycaonoides</td>
<td>30</td>
</tr>
<tr>
<td>Machairodontinae</td>
<td>Homotherium latidens</td>
<td>200</td>
</tr>
<tr>
<td>Machairodontinae</td>
<td>Megacynus whitei</td>
<td>100</td>
</tr>
<tr>
<td>Felinae</td>
<td>Lynx cf. pardina</td>
<td>18</td>
</tr>
<tr>
<td>Hyaenidae</td>
<td>Pachycrocuta brevirrostris</td>
<td>110</td>
</tr>
<tr>
<td>Homininae</td>
<td>Homo sp.</td>
<td>53</td>
</tr>
</tbody>
</table>

These mass estimates were recalculated with allometric equations (see chapters in Damuth and MacFadden, 1990) when new data were available for BL-D and/or FN-3.
paleocommunity (see Rodríguez-Gómez et al., 2014, 2015) were used. These indexes measure competition intensity among secondary consumers and are described in Section 2.2.4.

2.2.1. Total available biomass (TAB)

The model assumes that all of the variations in population size and composition may be taken as oscillations around a mean value that is constant through time. This constant value is the objective of the model. Leslie matrices (Leslie, 1945, 1948) are used to obtain average population profiles in the long-term. These techniques are used to model the dynamics of the population. Then, conditions of stability are written in terms of the matrices. These conditions provide the structure of a stable and stationary population over time (i.e., population age structure and body size are assumed to be constant from year to year).

The input data of the model are estimates of physical and physiological variables (i.e., adult and neonate body mass, litter size, breeding interval, age at reproductive maturity, growth rate and lifespan) for the species of large mammals preserved in the sites. These estimates are species-specific and allow the computation of population and mortality profiles for each species of primary consumers, from which estimates of the average sustainable biomass output by age classes are obtained. Each dead individual is assigned to one of six size categories according to its average body mass at age of death: 10–45 kg, 45–90 kg, 90–180 kg, 180–360 kg, 360–1000 kg, and >1000 kg (see Rodríguez et al., 2012). The annual biomass available for secondary consumers from each single primary consumer population is computed taking into account, for each age class, the mortality rate and the average body mass of those individuals that belong to this age class (for subadult age classes, body mass is obtained from body weight at birth and growth rate).

The model yielded several population profiles for each species, corresponding to different mortality rates. We selected extreme values with maximum and minimum pressure on sub-adults (or maximum and minimum mortality rates) that produced minimum and maximum TAB levels (TAB-m and TAB-M, respectively). The mortality rate accounts for the number of individuals of each age class that die every year in a sustainable population, whatever their causes of death (i.e., predation, illness, or accidents). Therefore, the predation rate is a fraction of the mortality rate. In our model, the biomass available for secondary consumers includes only prey in the case of hypercarnivores with primary access to ungulate carcasses (i.e., felids and painted dogs), as we consider that these species did not consume carrion (which means that predation rate equals mortality rate for their prey species). However, in the case of those carnivores with secondary access to ungulate carcasses (i.e., giant hyena, bear, small canids, and Homo sp.), carrion was considered as their main source of flesh with independence of the

![Graph A: Proportion of ungulate meat in the diet of the secondary consumers of BL-D and FN-3](image-a)

![Graph B: Total nutritional requirements of secondary consumers (NR, in kcal/km²/year) distributed among ungulate size categories](image-b)

![Graph C: Proportional predation pressure (PPP) of secondary consumers on each ungulate size category](image-c)

Fig. 2. A: Proportion of ungulate meat in the diet of the secondary consumers of BL-D and FN-3 (the remaining fraction represents the contribution to their diet of mammals weighing <10 kg, birds, reptiles, amphibians, and/or plant resources). B: biomass demanded (kcal/km²/year) by the populations of secondary consumers under optimal conditions (i.e., maximum ecological density) from each ungulate size category according to the profiles of prey preferences estimated for these species. C: proportional predation pressure (PPP) of secondary consumers on each ungulate size category.
causes of death for the ungulates scavenge.

Given that the model solutions do not depend on population size, it was necessary to estimate the population density of each primary consumer species. We used the equation provided by Damuth (1981) for European mixed temperate forest ecosystems for all ungulate species included in the study:

$$\log (D) = -0.79 \times \log (m) + 4.33, \quad r^2 = 0.94,$$

(1)

where $D$ is population density in number of individuals per square kilometer and $m$ is body mass in grams.

It could be argued that: (1) the estimates of population density used in the model for ungulate species are based ultimately on the body mass estimated for these species, which in some cases don’t have direct analogues among modern ungulates; and (2) the actual abundances of the species as recorded in the fossil assemblages of BL-D and FN-3 could provide more direct estimates of their relative abundances on the paleocommunity. However, the fossil assemblages from BL-D and FN-3 show evidence of intense activity of scavenging carnivores and hominins on the skeletal remains of large mammals, as noted above. This means that the abundances of the ungulate species in the assemblages were intensely biased with respect to their original abundances in the paleocommunity and would not reflect their population densities. In the nearby site of VM, which has been more intensively excavated during the last decades and has a more complete record of large mammals than BL-D and FN-3 (Espigares, 2010), analyses of skeletal representation for ungulate species have shown a number of taphonomic biases in the assemblage, including: (1) the selection of specific ungulate prey profiles by the hypercarnivores (i.e., saber-toothed cats and painted dogs), which focused on juvenile individuals in the case of large-sized prey species; (2) the selective transport by hyenas of herbivore carcasses and body parts to the surroundings of their maternity dens as a function of the mass of the ungulates scavenge; and (3) the fracturing of major limb bones of ungulates in the dens, which was also highly selective and correlated well with their marrow contents and mineral density. As a result, important differences of preservational patterns were recorded among taxa (e.g., horse bones are better preserved than those of bison and deer given the higher marrow yields of the latter) as well as among the skeletal elements of each ungulate species (e.g., proximal limb bones such as humeri and femora are less represented than distal ones such as metapodials) (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001; Palmqvist et al., 1996, 2011). Taphonomic data for BL-D and FN-3 (Espigares, 2010) show similar biases in the large mammal assemblages unearthed from these sites, as most of the bones preserved show spiral fractures in their diaphyseal shafts that evidence that they were fractured in fresh state by the hominins (and, to a lesser extent, by the hyenas) as well as abundant cut-marks related to defleshing activities (and a lower proportion of carnivore gnaw-marks).

In any case, it should be noted that the abundance of an ungulate species in a fossil assemblage formed by attritional mortality would not reflect its abundance in the original community, even in those cases in which taphonomic biases were absent. The reason is that, in the latter situation, species abundance in the assemblage would relate to the number of individuals of this species that died during the period of time when the assemblage was being formed. According to the model of Damuth (1982), this depends on population density, which scales to the $-0.75$ power of body mass, and also on population turnover rate (which can be estimated from birth rate, duration of postnatal growth, or the reciprocal of life expectancy at birth), which scales to the $-0.3$ power of body mass. As a result, species abundances in the assemblage (which can be estimated from NISP counts) would scale to the $-1.05$ power of their body masses, with a confidence interval for this exponent comprised between $-1.3$ and $-0.8$ (Damuth, 1982). If taphonomic biases were present, however, the slope obtained for the size/abundance relationship would be greater than the one expected, because those destructive processes that affect bone survival during the biostratigraphic stage (e.g., physico-chemical weathering and bone crushing by scavenging carnivores prior to burial in the sediment) depend on the relative surface of exposure of the skeletal elements to these agents, which results in the preferential destruction of those bone remains from small-sized species given their higher ratio of outer surface to inner volume.

In the case of BL-D and FN-3, an in-depth quantitative evaluation of the consequences of taphonomic biases on the composition of their fossil assemblages has not been addressed yet because the numbers of identifiable specimens for the large mammals species are not as high as in VM. In the latter site, the use of Damuth’s model showed that the original abundance of ungulates in the accumulated assemblage was severely biased by *P. brevirostris*. This giant hyena was identified as the bone-collecting agency at VM and consumed more intensively those skeletal remains from small-sized species, which showed more vulnerability to bone cracking (Palmqvist et al., 2011). As a result, the relative frequencies of the species preserved in the VM assemblage don’t fit the size/
abundance relationship that characterizes modern mammalian communities (Arribas and Palmqvist, 1998). Taphonomic evidence from BL-D and FN-3 (Espigares, 2010) points to similar biases in the abundance of ungulate taxa to those described for VM. In addition, huge lithic assemblages of Oldowan tradition and abundant evidence of hominin activity on large mammal bones, which are both absent from VM, have been preserved in both sites, including the finding in FN-3 of a dismembered carcase of elephant Mammutthus meridionalis that is surrounded by flint flakes and hyena coprolites (Espigares et al., 2013). In these sites, modification of bones produced by carnivores, mainly hyenas, is also present, but it is less abundant than human modification and the degree of anatomical connection between skeletal elements is higher than in VM (Espigares, 2010). All this evidence suggests that flesh-eating predators (e.g., saber-toothed cats) had primary access to the ungulate carcasses followed by the hominins and, less frequently, other scavenging carnivores such as the hyenas. As a result, the frequencies of the ungulate species preserved in the fossil assemblages from BL-D and FN-3 were highly biased compared to their natural abundance in the paleocommunity. For this reason, it is more realistic to estimate the original population densities of these species using the "taxon-free" regression equations derived by Damuth (1981) for primary consumers in European mixed temperate forest ecosystems, as indicated above.

2.2.2. Total demanded biomass (TDB)

The first step for evaluating the distribution of resources among secondary consumers is to estimate the amount of resources demanded by each species. Intake rate was estimated for each secondary consumer using the equation provided by Farlow (1976):

$$\log I = (0.70962) \log (m) + 0.27747; \quad r^2 = 0.97,$$

where $I$ is intake rate in kilocalories per day and $m$ is body mass in grams. Note that the slope used in this study is the maximum value of the range provided by Farlow (1976) for the slope $(0.69686 \pm 0.01276)$. We made a number of adjustments for some secondary consumers according to their inferred dietary preferences, based on Rodríguez et al. (2012) (Table 2, Fig. 2A). We estimated that ungulate flesh represented 20% of the energetic requirements of C. mosbachensis, 10% for Lynx cf. pardinus, 30% for Homo sp., 98% for P. brevirostris (because 2% of the total requirements could be obtained from bone marrow), and 10% for Ursus etruscus. In the case of L. lycanoaoides, H. latidens and M. whitei, we assumed that flesh represented 100% of the energetic requirements of these predators (Palmqvist et al., 2003, 2007, 2008a, 2008b). The mean daily requirements of Homo sp. were estimated in 2700 kcal per individual. This value is similar to those of recent hunter-gatherer populations, 3000 kcal per individual (Eaton et al., 1997), and was corrected for the smaller body mass estimated for this population of Homo sp. (53 kg, average of the mass estimates provided for early Homo by Jiménez-Arenas et al., 2014).

The annual energetic requirements of each carnivore population per square kilometer (Fig. 2B) were obtained multiplying individual annual intake by population density. The equation provided by Damuth (1993) for African flesh-eaters in open environments was used to estimate typical carnivore densities:

$$\log (D) = -0.64 \times \log (m) + 2.23; \quad r^2 = 0.36,$$

where $D$ is population density (individuals/km²) and $m$ is body mass (g). The equation for African flesh-eaters was used instead of the equation provided in the same source for European and North American species for two reasons. First, living African species are better ecological analogues for the Late Villafranchian carnivores than living Holarctic carnivores. And second, the correlation coefficient of the equation for Holarctic carnivores provided by Damuth (1993) is not significant. Population density for Homo sp. was estimated as the value of maximum density for populations of recent hunter-gatherers, 0.24 individuals per square kilometer from the Hadza population (Binford, 2001) (see Table 1 in Rodríguez-Gómez et al., 2013).

As in the case of TAB, TDB was distributed over the six body size categories cited above, based on the prey size preferences of each predator inferred from the behavior of their living relatives (Table 2) (Rodriguez et al., 2012) and also using inferences on prey preferences obtained with isotopic data for the species preserved in the VM site (Palmqvist et al., 2008b). The preference of a predator for a body size category is represented by the percentage of predation (PD) that this size category was presumed to represent in its diet. If a secondary consumer was presumed to be unable to kill prey from a given size category and was considered as a primary predator (i.e., it was assumed that this species did not consume carrion, as in the case of L. lycanoaoides or the felids), a PD of 0 was assigned to this predator for this size category. It is important to note that PD represents the “a priori” prey preferences of each carnivore, but the final contribution of a prey category to the diet of a given predator is an output of the model, and it is modulated by prey availability and competition with other carnivores.

2.2.3. Distribution of TAB among secondary consumers

TAB was distributed between secondary consumers based on the proportional predation pressure ($PPP_j$) of each carnivore species over each body size category (Fig. 2C), which represents the relative amount of biomass demanded by the $j$th species of secondary consumers from the $i$th size category of primary consumers. $PPP_j$ is calculated as the proportion of the total amount of biomass demanded from a prey size category by each carnivore and allows incorporating intraguild competition in the model. The distribution of TAB finished when: (1) all secondary consumers fulfilled their requirements; or (2) when the entire TAB was consumed. This distribution of TAB was then translated into sustainable densities or estimated densities ($Dsj$) for each species of secondary consumers (for a detailed formal description of resource distribution computation, see Rodríguez-Gómez et al., 2013, 2014, 2016a, 2016b).

2.2.4. Competition intensity indexes

The indexes used in this study are based on the densities estimated and expected for secondary consumers, and they try to measure the amount of requirements unsatisfied both at the species level and at the guild level. The “dissatisfaction degree” is a measurement of competition intensity: when competition increases, it is more difficult for a carnivore to obtain resources and the amount of unsatisfied requirements is higher. It is assumed that a species will only fulfill its requirements and reach its expected density if it suffers a weak competition. Under this point of view, we used three indexes based on: (1) the expected vs. estimated density for each species (”Species Competition Index”, SCI); (2) the expected vs. estimated density for the whole carnivore guild (”Global Competition Index”, GCI); and (3) the expected vs. estimated biomass of the carnivore guild (”Global Competition Index Biomass”, GCB) (Rodríguez-Gómez et al., 2012). The mathematical model estimates the sustainable densities for each secondary consumer while the expected densities are estimated from Damuth’s allometric equations (Table 2).

The species competition index (SCI) was computed as:

$$SCI_j = 1 - (Dsj/Dxj)$$

where $Dxj$ is the expected density for the $j$th species (obtained from...
the allometric equation in Damuth, 1993) and $D_{sj}$ is its estimated density (obtained from the model). Therefore, this index measures to what degree a species fulfills its dietary requirements in a given environment. SCI values were derived separately from TAB-m and TAB-M estimates (SCI-m and SCI-M values, respectively).

The global competition index (GCI), which measures competition intensity at the level of the carnivore guild, was obtained from:

$$GCI = 1 - \frac{\sum_{j=1}^{n} D_{sj}}{\sum_{j=1}^{n} D_{xj}}$$

where $D_{sj}$ and $D_{xj}$ are the estimated and expected densities for the $j$th species, as noted above. We obtained GCI values for TAB-m and TAB-M estimates (GCI-m and GCI-M values, respectively).

The global competition index biomass (GCIB) was computed as:

$$GCIB = 1 - \frac{\sum_{j=1}^{n} D_{sj} * W_j}{\sum_{j=1}^{n} D_{xj} * W_j}$$

where $W_j$ is the body mass of the $j$th species of the carnivore guild, while $D_{sj}$ and $D_{xj}$ are the densities described above. This index shows the degree to which the guild of secondary consumers reaches the optimal biomass. As in the preceding cases, we obtained a GCIB value for TAB-m and another for TAB-M (GCIB-m and GCIB-M values, respectively).

These indexes provided information on the degree of competition intensity in the ecosystem compared to an ideal condition in which all species would reach optimal densities and levels of population biomass. The closer the value of an index is to 1, the higher is the competition among the secondary consumers. In contrast, index values close to 0 indicate a low degree of competition for dietary resources.

### 3. Results

The model estimates the biomass provided by the species of primary consumers preserved in BL-D and FN-3 as the total available biomass (TAB). The minimum value of TAB (TAB-m), which corresponds to the maximum rate of sub-adult mortality, is 410,904 kcal/km² per year for these sites, and the maximum value of TAB (TAB-M), which results from the minimal rate of sub-adult mortality, is 575,454 kcal/km² per year (i.e., TAB-m is 29% lower than TAB-M). These estimates show that the ungulate biomass available for the secondary consumers was much lower than the one demanded under optimal conditions (i.e., the energetic demands of all species if they reached their maximal population densities), which is estimated by TDB (1051,606 kcal/km² per year).

In order to know which ecological densities could be supported in the paleoecosystem of BL-D and FN-3 for the species of the carnivore guild, it is necessary to compare the supply of resources with their demands (TAB and TDB, respectively). This comparison indicates that the ecosystem could hold, in the interval between TAB-m and TAB-M, and for an area of 100 km² during a year, 17–25 individuals of *C. mosbachensis*, 10–14 of *Homo sp.*, 9–16 of *Lynx cf. pardinus*, 9–10 of *L. lynxoides*, 4–6 of *P. brevirostris*, 4–5 of *M. whitei*, 3–4 of *H. latidens*, and 2–3 of *U. etruscus* (Table 3). These sustainable densities would allow a viable ecosystem for BL-D and FN-3, as they are above the values of MVPD (Minimum Viable Population Density) obtained using the allometric equations of Silva and Downing (1994) (Table 3).

### Table 4

Global Competition Index (GCI) and Global Competition Index Biomass (GCIB) for BL-D and FN-3. TAB-m: minimum total available biomass; TAB-M: maximum total available biomass.

<table>
<thead>
<tr>
<th>Index</th>
<th>TAB-m</th>
<th>TAB-M</th>
</tr>
</thead>
<tbody>
<tr>
<td>GCI</td>
<td>0.58</td>
<td>0.50</td>
</tr>
<tr>
<td>GCIB</td>
<td>0.59</td>
<td>0.45</td>
</tr>
</tbody>
</table>

The indexes that measure competition intensity within the carnivore guild of BL-D and FN-3 show values that are above 0.50 in all cases (Table 4), which indicates that less than half of the requirements demanded for GCI-m and GCIB-m under optimal conditions with maximal population densities would be satisfied. Specifically, the value of the GCI-m index (0.58) indicates that less than half the number of individuals of the species of secondary consumers expected could be supported by the ecosystem if the minimum value of total available biomass of ungulates is considered. However, this fraction could be reached if the maximum total available biomass was available, as indicated by the GCI-M index (0.50). Similarly, the value of the GCIB-m index (0.59) shows that the ungulate community would not support half the biomass of secondary consumers expected, although this would be achieved in the case of GCIB-M (0.45). The differences between the values of the GCI and GCIB indexes result from differences in the quantity of available biomass that depend on whether the mortality rate for sub-adults in the community of primary consumed is considered as minimal (TAB-m) or maximal (TAB-M). In addition, it should be noted that GCIB-m is greater than GCI-m because the biomass of the carnivore guild is displaced toward the secondary consumers of smaller body mass (e.g., the lynx), which means that the densities estimated with TAB-m for these species are greater than those calculated with TAB-M. Conversely, GCIB-M is lower than GCI-M because the TAB estimate shifts to the secondary consumers of larger size and this results in a reduction in the number of secondary consumers of small size that could be supported by the
ungulate community (Figs. 3–4, Table 3). The reason is that the rate of sub-adult mortality for primary consumers is minimal with TAB-M and the individuals reach larger body sizes that are unavailable for those secondary consumers of small body mass that do not show a scavenging behavior (e.g., the lynx and the pack-hunting dog).

Fig. 3 and Table 5 show the percentage of TAB consumed by each species of secondary consumers. These data indicate that the distribution of resources among the members of the carnivore guild is similar for TAB-m and TAB-M, and also that H. latidens and P. brevirostris are the species that consumed a greater fraction of the ungulate biomass available. In the case of TAB-m, P. brevirostris would consume ~93,000 kcal/km² per year and H. latidens ~87,000 kcal/km² per year (Table 3), which represent 23% and 21% of TAB-m, respectively (Table 5). This is in agreement with the habitat reconstruction performed by Mendoza et al. (2005) for VM, which showed a predominance of open plains with tree patches in the paleoenvironment of the basin during Calabrian times. This habitat would be favorable to H. latidens, the top predator of the paleocommunity, for which a coursing behavior in open plains has been deduced, and also for P. brevirostris, a scavenger that probably searched for ungulate carcasses in unforested habitat, as modern hyenas do (Palmqvist et al., 2003, 2008a, 2008b). The species that followed in the rank of resource consumption are the ambush dirk-toothed cat M. whitei and the hypercarnivorous canid L. lycaonoides (20% of TAB-m in both cases), Homo sp. (7%), C. mosbachensis (4%), U. eutrкус, and Lynx cf. pardinus (2% in both cases). If we consider TAB-M, H. latidens would be the carnivore with greater consumption (149,533 kcal/km² per year, 26%), followed by P. brevirostris (23%), M. whitei and L. lycaonoides (20% in both cases), Homo sp. (7%), C. mosbachensis (4%), U. eutrкус (2%) and Lynx cf. pardinus (1%). Given these estimates, the carnivore species could be divided in two groups, those that each of its constituent species consumed >16% of TAB and those that each obtained <7% of TAB.

If we analyze to which extent the demands of each carnivore species are met (i.e., the percentage of its dietary requirements that are satisfied, SCI; see Table 3 and Fig. 4), different patterns are observed for minimal and maximal TAB values. Specifically, for TAB-m there is a “ceiling effect” in the values of SCI-m close to 0.70 (Fig. 4). However, for TAB-M there is a more scattered SCI-M pattern and the “ceiling effect” vanishes. It can also be observed that C. mosbachensis, Homo sp., H. latidens, P. brevirostris, and U. eutrкус are the species that show lower SCI values for TAB-M (Table 3), which means that they would cover their dietary requirements to a greater extent than the other carnivores. The species less affected by the conditions of TAB-m and TAB-M is L. lycaonoides, which shows SCI values of 0.62 and 0.56, respectively. In contrast, the carnivore more affected is H. latidens, with SCI-m and SCI-M values of 0.63 and 0.36, respectively. All species decrease their SCI values from TAB-m to TAB-M except Lynx cf. pardinus, which is the carnivore that satisfies to a greater extent its dietary requirements for the condition TAB-m and shows the lowest SCI-m value (0.51).

In contrast, this species has the highest SCI-M value (0.71) among the carnivore guild. Homo sp. is affected by the differences in sub-adult mortality for primary consumers (i.e., TAB-m vs. TAB-M) to the same extent than most species of secondary consumers (C. mosbachensis, P. brevirostris and U. eutrкус) (Table 3). In any case, it is interesting that the SCI values of Homo sp. are among the lowest obtained in the carnivore guild, especially in the case of SCI-M. This can be tentatively interpreted as evidencing that the hominins behaved more as opportunistic scavengers than as hunters, as suggested by other authors. In fact, if they behaved as primary predators they would presumably compete for a relatively narrow prey size range. This would in turn increase the level of intraguild competition for these resources, which would imply that the hominins had access to a lower amount of resources, and this would ultimately result in a lower population density for them. Of interest to this study, a recent network analysis of food webs in the European Early and Middle Pleistocene (Lozano et al., 2015) has suggested that the Late Villafranchian hominins were likely opportunistic omnivores that occupied a central position in the
food web, as in the case of *C. mosbachensis*. This is in contradiction with the interpretation of a small effect of the arrival of *Homo* sp. in Europe on the structure of food webs and of a marginal role of the hominins in the paleocommunity (see discussion in Lozano et al., 2015).

Finally, the results obtained in the three strategies tested for *Homo* sp. (i.e., hunting, scavenging and hunting plus scavenging) don’t provide clear insights on which of them would have allowed the hominins to reach a higher population density and could thus be considered as the optimal for food acquisition in the Early Pleistocene of Southeast Spain. In fact, the estimates of population densities of hominins obtained for the three procurement strategies considered are similar (Table 6), although it should be noted that the population density reached with a hunting strategy is lower than the estimates obtained with the two other strategies.

4. Discussion

The Late Villafranchian (Calabrian, Early Pleistocene) sites of Orce (Baza Basin, SE Spain) are key to understanding the ecological context in which the first human dispersal out of Africa took place. Our analysis offers information on the environment inhabited by the earliest hominin settlements in Western Europe, which is crucial for deciphering the interactions of these human populations with the environment and the large mammal species with which they lived after their arrival in the European subcontinent (Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1999; Palmqvist et al., 2003, 2005, 2008a, 2008b; Mendoza et al., 2005; Martínez-Navarro, 2010; Espigares et al., 2013; García-Aguilar et al., 2014, 2015; Martínez-Navarro et al., 2014). This study, which is based on mathematical tools widely used in population dynamics (Owen-Smith, 2010), provides a new approach for evaluating the sustainability of the community of secondary consumers based on the biomass of primary consumers potentially available.
Our analysis of the fossil assemblages preserved at the sites of Barranco León-D (BL-D) and Fuente Nueva-3 (FN-3) shows a community of large mammals with a relatively high diversity of secondary consumers that would satisfy slightly less than half of their dietary requirements under optimal ecological conditions (i.e., those in which they would reach their maximal population densities). According to the results obtained, under the less favorable conditions (i.e., TAB-m), an area of 100 km² in the Baza Basin could contribute 30% of Homo sp. (see Table 2 for the abundances of ungulate prey size profiles considered in them).

Table 6
Estimated ecological densities (individuals per km²) for the species of secondary consumers of BL-D and FN-3 in two different scenarios (TAB-M and TAB-m) according to three different procurement strategies for Homo sp. (see Table 2 for the abundances of ungulate prey size profiles considered in them).

<table>
<thead>
<tr>
<th>Species and ecological scenarios</th>
<th>Scavenging Homo sp.</th>
<th>Hunting Homo sp.</th>
<th>Scavenging—hunting Homo sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>TAB-m</td>
<td>TAB-M</td>
<td>TAB-m</td>
</tr>
<tr>
<td>Ursus etruscus</td>
<td>0.02</td>
<td>0.03</td>
<td>0.02</td>
</tr>
<tr>
<td>Canis mosbachensis</td>
<td>0.17</td>
<td>0.25</td>
<td>0.18</td>
</tr>
<tr>
<td>Lycaon lycaonoides</td>
<td>0.09</td>
<td>0.10</td>
<td>0.09</td>
</tr>
<tr>
<td>Pachycrocuta brevirostris</td>
<td>0.03</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>Homo sp.</td>
<td>0.04</td>
<td>0.06</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>0.10</td>
<td>0.14</td>
<td>0.09</td>
</tr>
</tbody>
</table>

Five species show greater demands of resources and higher levels of consumption of TAB among the community of secondary consumers: *H. latidens*, *L. lycaonoides*, *M. whitei*, and *P. brevirostris* (Fig. 3 and Table 5). The other species, *C. mosbachensis*, *Homo sp.*, *Lynx cf. pardinus* and *U. etruscus*, would play a more secondary role in the paleoecosystem in which concerns the consumption of TAB. The percentages of TAB consumed by the members of the carnivore guild show similar patterns for TAB-m and TAB-M, although the greater differences are found in *H. latidens*, *L. lycaonoides* and *Lynx cf. pardinus*. The first species increases its weight in the community with TAB-M compared to TAB-m, and this is the carnivore that has a greater consumption followed by *P. brevirostris*, a situation that is reversed for TAB-m. In the case of *L. lycaonoides* and *Lynx cf. pardinus*, both species reduce their percentages of consumption from TAB-m to TAB-M. These species are influenced by the differences in mortality rates for sub-adult ungulates: while *H. latidens* is benefited when a greater proportion of primary consumers reach the adult stage, *L. lycaonoides* and *Lynx cf. pardinus* are in disadvantage under such circumstances. The reason is that only *H. latidens* and the scavengers would presumably consume the carcasses of megaherbivores (i.e., those species in excess of 1000 kg, which are included in the sixth category of primary consumers). Given that this ungulate size category is the one that provides greater biomass, these carnivores can consume more resources from megaherbivores under the TAB-M conditions. In fact, biogeochemical analyses in the Venta Micena site have shown that very large prey were relatively minor components of the diet of all hypercarnivores except *H. latidens* and the scavenging *P. brevirostris* (Palmqvist et al., 2003, 2008a, 2008b).
In which concerns the SCI values (Table 3 and Fig. 4), Lynx cf. pardinus is the species that satisfies to a greater extent its dietary requirements for TAB-m, showing the lowest SCI values, but this situation is reversed for TAB-M. The reason is that when we only consider the minimum proportion of sub-adult ungulates (TAB-M), the biomass is displaced toward larger size categories and there is less prey available for this small-sized predator. The species less affected by the conditions depicted by TAB-m and TAB-M is *L. lycaonoides*, which shows SCI values of 0.62 (SCI-m) and 0.56 (SCI-M). This result is explained by a high competence with other secondary consumers in both situations (i.e., TAB-m and TAB-M) for the ungulates preyed upon by *L. lycaonoides* (adult *Hemitragus* and juvenile *Equus* according to isotopic data in Palmqvist et al., 2008b), which agrees with data on modern African painted dogs (Gorman et al., 1998; Carbone et al., 2005), their modern closest relatives. The SCI values obtained show that the scavengers and *H. latidens* are the species that satisfy to a greater extent their dietary requirements. *Homo* sp. has been modeled in this study as an omnivore with secondary access to ungulate carcasses. These results seem to confirm that a scavenging behavior would have been optimal for these human populations, because when a primary access was considered the degree of satisfaction of the flesh requirements of *Homo* sp. decreased, as reflected in the lower estimate of population density obtained (Table 6).

The GCI and GCIB indexes (Table 4) show that the community of secondary consumers would not be close to half the values expected for population density and biomass under TAB-m conditions, with values for GCI-m and GCIB-m of 0.58 and 0.59, respectively. In the case of TAB-M, half the biomass and density expected would be surpassed and equaled, respectively, with values of 0.45 for GCIB-M and 0.50 for GCI-M. The differences between the values for GCI and GCIB show the effects of the distribution of resources taking into account the biomass expected for the community of secondary consumers (Rodríguez-Gómez et al., 2012). GCIB shows a pattern similar to that of GCI. However, this index takes into account not only the density of species, but also the biomass of individuals. The higher value of GCIB-m compared to GCI-m results from the fact that a slightly greater fraction of TAB is skewed towards the larger species. In contrast, the value obtained for GCIB-M is lower than the corresponding one for GCI-M, which means that the investment in large-sized species is more important. If GCIB and GCI were equal, there would be a more proportionate distribution of resources among species, because the mass of species would have no effects and resource distribution would be weighed up by ecological density.

During the last decades, there has been a growing consensus in assuming that hominins dispersed in Western Europe during the late Early Pleistocene (Calabrian), as evidenced by the paleoanthropological remains and tool assemblages recovered from a number of sites dated below the Jaramillo subchron (e.g., BL-D, FN-3 and TE9 in Spain, Pirro Nord in Italy; Dennell and Roebroeks, 1996, 2005; Arribas and Palmqvist, 1999; Arzarello et al., 2007; Carbonell et al., 2008; Jiménez-Arenas et al., 2011b; Toro-Moyano et al., 2013; but see Muttoni et al., 2011, 2013, 2015). However, given the scarcity of the hominin record in Europe during these chronologies, a new debate has arisen in the last years on whether human presence was continuous after the initial settlement or was intermittent, with multiple dispersal events of populations constrained by climatic and ecological fluctuations (Agustí et al., 2009; Dennell et al., 2011; Leroy et al., 2011; MacDonald et al., 2012; Bermúdez de Castro and Martínón-Torres, 2013; Bermúdez de Castro et al., 2013; Rodríguez et al., 2015a, 2015b; Rodríguez-Gómez et al., 2014; Rodríguez-Gómez, 2015).

The results of this study can shed light on this debate. Specifically, the values of the GCI and GCIB indexes obtained for the Orce sites are above those of the stratigraphic levels analyzed of the sites of Gran Dolina and Galería in Atapuerca, NW Spain (Rodríguez-Gómez et al., 2016a). The chronology of the latter levels ranges between ~1.0 and ~0.2 Ma (Falguères et al., 2013; Rodríguez et al., 2011) and is younger than the age estimated for the faunal assemblages of BL-D and FN-3, ~1.5–1.2 Ma (Duval et al., 2012; Toro-Moyano et al., 2013; Álvarez et al., 2015; Palmqvist et al., 2016). The levels of Atapuerca provided GCI and GCIB values below 0.37 and 0.38, respectively. In all these cases, the secondary consumers would reach more than half of the expected density and biomass. In fact, these values were higher than two thirds of the expected ones in most cases (i.e., values of GCI and GCIB below 0.33).

The GCI and GCIB values estimated here for the large mammal assemblages of FN-3 and BL-D are higher than 0.50 in all cases, with the only exception of the GCIB value obtained for the TAB-M scenario (0.45). Compared with the faunal assemblages from the Atapuerca TD levels, the greatest differences were found for TD6-2, the level that showed the minimum GCI and GCIB values, and to a lesser extent for TD-8, although it should be noted that these differences decreased in two hypothetical scenarios: TD6-2 with two large felids and TD8 with a population of *Homo* sp. (Rodríguez-Gómez et al., 2016a). However, even these hypothetical scenarios showed lower competition intensities than FN-3 and BL-D.

The sharp contrast between the values obtained for the competition indexes in the Atapuerca levels and the Orce sites results from the higher diversity of secondary consumers and the greater complexity of ecological relationships among the members of the carnivore guild in the latter sites. This probably relates to the abundance of hot springs linked to tectonic activity in the lacustrine environments of the Baza basin during the Pleistocene. Such ‘ecological islands’ of thermal waters attracted many species and were advantageous for hominin settlements, as evidenced by a number of Plio-Pleistocene sites of the African Rift Valley found in similar paleoenvironmental contexts (García-Aguilar et al., 2014, 2015).

At a European scale, however, the values estimated for GCI and GCIB for the sites dated between 1.1 and 0.8 Ma were closer to those found here for BL-D and FN-3 (Rodríguez-Gómez, 2015). Of these sites, the Middle Unit of Vallparadís and the level III of Grotte du Vallonnet showed values that are close to those of BL-D and FN-3: 0.65 and 0.58 for GCI-m, 0.55 and 0.46 for GCI-M, 0.62 and 0.58 for GCIB-m, and 0.48 and 0.43 for GCIB-M, respectively. The level 12 of the site of Kozarnika, however, shows values that are above those of the Orce localities (0.74, 0.69, 0.73, and 0.65, respectively; Rodríguez-Gómez, 2015). Therefore, the results obtained for BL-D and FN-3 lie within the group of sites that show high levels of competition intensity between the members of the carnivore guild. These results are in agreement with the trend to decreasing the intensity of ecological competition from the latest Early Pleistocene to the Middle Pleistocene in different regions of Europe, as proposed by a number of researchers (e.g., Meloro et al., 2007; Palombo, 2010; Raia et al., 2007; Rodríguez et al., 2012). Moreover, the increase in the number of archaeological sites at this time (see Mosquera et al., 2013 and references therein) provides evidence on a more intense occupation of the European landscapes by human populations from Middle Pleistocene times onwards.

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