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RESEARCH

Carrying capacity and meat availability for the Neanderthal groups in the upper valley of the Lozoya River (Madrid, Spain): a key region for the study of their ecosystems in Central Iberia

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Abstract

Located in the upper valley of the Lozoya River, Cueva del Camino (Madrid, Spain) is one of the richest Early Pleistocene paleontological sites in the Iberian Peninsula. The results of the work carried out over the last three decades have led to the interpretation of the site as a hyena den with intermittent human presence. The faunal assemblage of layer 05 of Cueva del Camino dates to about 90 ka (MIS 5c) and includes small, medium, and large mammals. The presence of lithic industry and Neanderthal remains provide valuable insights into the strategies of past human groups in their access to animal resources. This study aims to determine the ecological conditions and availability of meat resources in the large mammal paleocommunity of Cueva del Camino by estimating carrying capacity (CC) and meat availability (TAB) in the upper valley of the Lozoya River. The estimates show a predominance of species with extreme body masses (either very small or very large) for CC, while TAB is mostly concentrated in small species. To evaluate and contextualize these estimates, the results were compared with other Pleistocene paleoecosystems of the Iberian Peninsula and with modern ecosystems. The upper valley of the Lozoya River reflects similar conditions to some Pleistocene faunal assemblages in Sierra de Atapuerca, such as Gran Dolina and Galería, and to the Serengeti National Park in the case of modern ecosystems. Based on density estimates and population size, the upper valley of the Lozoya River closely resembles populations of contemporary hunter-gatherer groups, and its conditions may have been sufficient to support a Neanderthal group of approximately 34 individuals.

Keywords Cueva del Camino · Pinilla del Valle · Late Pleistocene · Large mammals · Paleoecosystems · Human ecology

Introduction

Resource availability is an important factor concerning the survival and distribution of species. In the case of human populations, it is widely known that meat resources have played a pivotal role for a significant part of our evolutionary history, especially for European Pleistocene lineages (Speth 1987; Roebroeks 2001; Hublin and Richards 2009; Ferraro et al. 2013). It is stated that meat resources constituted an important part of the Neanderthal diet (Richards et al. 2000; Bocherens et al. 2005; Hublin and Richards 2009; Richards and Trinkaus 2009; Churchill 2014; Smith 2015; Rendu

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et al. 2019; Marín-Arroyo and Sanz-Royo 2022). However, many studies show that they had a diverse diet and consumed large amounts of plant resources (Stringer et al. 2008; Cortés-Sánchez et al. 2011; El Zaatari et al. 2011; Henry et al. 2011, 2014; Hardy et al. 2012; Sistiaga et al. 2014; Estalrrich et al. 2017; Power et al. 2018; Fiorenza et al. 2020; Zilhao et al., 2020; Salazar-García et al. 2021). Assuming that large mammals were a food source for Pleistocene human groups, their abilities to obtain these would be conditioned by ecological traits, abundance of prey and competition with other large carnivores (Bermúdez de Castro, 1995; Fariña, 1996; Palmqvist et al. 2003; Vizcaíno et al. 2004, 2010; Raia et al 2007; Meloro and Clauss 2012; Rodríguez-Gómez et al. 2013, 2014a, 2017c, 2024a). Delving deeper into the ecological frameworks in which human groups developed is a useful way to provide more insight into their subsistence strategies and the exploitation of resources. This is considered as key in the study of the evolution of human behavior (e.g., Kahlke and Gaudzinski 2005; Stringer et al. 2008). For this reason, it is essential to emphasize the importance of the following concepts: carrying capacity (CC) and meat availability (TAB, total available biomass). These are two indexes of great utility when characterizing ecosystems and paleoecosystems (e.g., Schaller 1972; Coe et al. 1976; Owen-Smith 1988; Hayward et al. 2007; Rodríguez-Gómez et al. 2013, 2014a, 2024a, b; Hatton et al. 2015; Rodríguez et al. 2014; Domingo et al. 2017a, b, among others). The concept of CC is widely used in life sciences and has been applied to a wide range of analysis levels varying from molecular to ecological studies (see Sayre 2008). In present ecosystems, CC has been used to study the conditions of ecological populations of large mammals and how they manage to preserve their populations (Schaller 1972; Owen-Smith 1988; Hayward et al. 2007). This study uses the third meaning of carrying capacity defined by Sayre (2008) as the "intrinsic limit of a population increase in organisms" (Sayre 2008, p. 120). When applied to paleoecological studies, it is useful to determine the trophic networks between predators and preys by obtaining accurate biomass estimations (Palmqvist et al. 2003; Barnosky 2008; Sayre 2008; Rodríguez et al., 2014; Rodríguez and Mateos, 2018; Kindler et al. 2020; Rodríguez-Gómez et al. 2022a, 2024a, b). In this study, CC is used as a synonym for the biomass of prey species that an ecosystem can sustain continuously, as proposed by Coe et al. (1976), i.e., without considering the carnivore biomass, in order to analyze the relationship between predator and prey biomass (see Rodríguez-Gómez et al. 2024a). It also should be taken into account that the concept of carrying capacity is often used as a synonym for meat resources available in ecosystems (e.g., Vidal-Cordasco et al. 2022, 2023). However, several studies support the use of the concept of available meat as the biomass that comes from ecosystems and that could be used sustainably by secondary consumers, since the CC could not be completely consumed without causing the ecosystem to collapse (Rodríguez-Gómez et al. 2013, 2014a, 2016b, 2017a, b, c, 2020, 2024a, b). Therefore, the concept of available meat refers to the biomass of primary consumers potentially available to secondary consumers, called TAB in Rodríguez-Gómez et al. (2014a). Approximations based on species survival and mortality profiles can be used to estimate both CC and TAB. These profiles help reconstruct the groups of species that developed in the same environment as humans (Rodríguez-Gómez et al. 2013, 2014a, 2016a, b, 2017a, b, c, 2022b, 2024a, b). Survival profiles are the proportion of individuals that survive by age group in a population. These allow to reconstruct the structure of the populations and to estimate the capacity of the ecosystem to maintain its respective fauna (Laws 1966; Mentis 1970; Coe et al. 1976). Mortality profiles are the proportion of individuals that die by age group in a population. Based on these mortality profiles under stability and stationarity conditions (see Martín-González et al. 2016; 2019), the availability of meat resources in the paleoecosystems in the long term can be estimated (Rodríguez-Gómez et al. 2012, 2013, 2014a, 2016a, b, 2017a, b, c, 2020, 2022a, b, 2024a, b). Mortality profiles include subadult individuals into the estimates, which was not traditionally considered in paleontology studies, and it could cause overestimations of the population biomass values (Rodríguez-Gómez et al. 2022a). This may be an aspect of interest for CC and TAB estimates, as body size is a key factor in predator–prey selection (Palmqvist et al. 1996; Carbone et al. 1999; Radloff and Du Toit 2004; Ercoli et al. 2014), and carnivore species may not have access to adult individuals of megaherbivore species, but do have access to subadults (Palmqvist et al. 1996; Palmqvist and Arribas 2001). There are mathematical models that allow to estimate survival and mortality profiles such as the Leslie-Lewis matrices or the Weibull model, which make projections of demographic parameters, making it possible to estimate life structures of fossil populations and to model their dynamics (Martín-González et al. 2016, 2019; Pérez-Pérez et al. 2021; Rodríguez-Gómez et al. 2022a, 2022b).

From a current perspective, one of the periods of great interest in studying climate and human evolution is the Last Interglacial (Marine Isotope Stage 5, MIS 5), as it is considered to represent the last epoch with a climate analogous to that of present-day Earth, prior to human impact (Antoine et al. 2024). MIS 5 was a period of minimal ice volume, extending from about 130 to 75 ka BP (Sánchez Goñi, 2007). Most of the information on the paleontological and paleoenvironmental record of this period comes from sites in northern and central Europe (e.g., Turner 2000; van Kolfschoten 2000; Kahlke 2002; von Koenigswald 2007; Locht et al. 2010; Pop 2014; Antoine and Locht 2015; Pop and Bakels 2015; Sier et al. 2015; Kindler

et al. 2020; Weiss et al. 2022). Although the Iberian Peninsula is one of the key regions for the study of the European Palaeolithic record due to its rich archaeological and paleontological heritage, there is a scarce representation of MIS 5 archaeological sites in the central region, having been found mainly in regions close to the coast (Fig. 1). This central region comprises two plateaus and a mountain system called Sistema Central, which presented unfavorable ecological conditions for human habitation in different periods of the Paleolithic (Burke et al. 2017; Wolf et al. 2018; Sala et al. 2020). Therefore, the presence of human populations in this area may have been discontinuous and limited, although in other periods it may have been favorable for human presence (Buitrago Villaplana 1992).

Cueva del Camino is an archaeo-paleontological site located in the upper valley of the Lozoya River (Madrid, Spain) of the Sistema Central with a very rich record of MIS 5 fauna and flora associated with *Homo neanderthalensis* remains (Arsuaga et al. 2012). Álvarez-Lao et al. (2013) argue that the Cueva del Camino record is of particular interest because it is one of the most complete from Central Iberia during MIS 5, providing relevant information on the paleontological, paleoecological, and paleoenvironmental conditions of this region during this period. From the yield

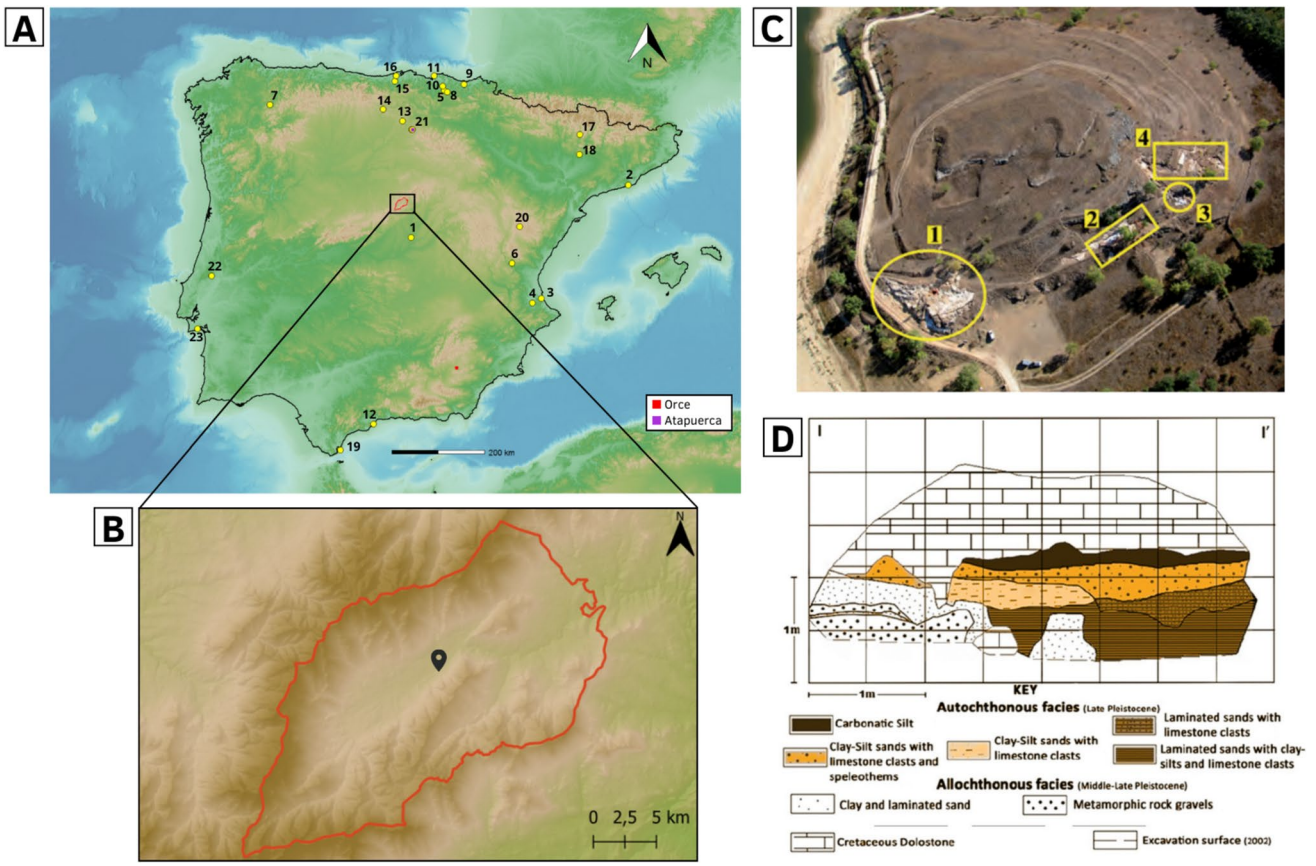

Fig. 1 **A** Location in the Iberian Peninsula of the Upper Lozoya River Valley, archaeological sites of MIS 5 and the sites of Orce and Atapuerca mentioned in the text. **B** Area (434.58 km2) of the upper Lozoya River valley. **C** Location of the sites in Calvero de la Higuera from Sánchez-Romero et al. (2017): 1. Cueva del Camino; 2. Navalmaíllo Rock Shelter; 3. Buena Pinta Cave; and 4. Des-Cubierta Cave. **D** Stratigraphic section along grids Z6-Z9 modified from Pérez-González et al. (2010) and Arsuaga et al. (2012). Archaeological sites corresponding to the numbers in A: 1. HAT (Sesé et al. 2011); 2. Cova del Rinoceront (Daura et al. 2015); 3. Bolomor Cave (Fernández-Peris et al. 2020); 4. Cova Negra (Real et al. 2023); 5. Axlor (Demuro et al. 2023); 6. Abrigo de la Quebrada (Real et al. 2023); 7. Valdevara 3 (Vaquero et al. 2018); 8. Lezetxiki I (Falgueres et al. 2005) and Lezetxiki II (Garcia-Ibaibarriaga et al. 2018; Rofes et al. 2012); 9. Amalda III (Rios-Garaizar et al. 2024); 10. Arlampe (Rios-Garaizar et al. 2015); 11. Aranbaltza III (Rios-Garaizar et al. 2018); 12. Bajondillo (Cortés-Sánchez et al. 2011); 13. Valdegoba (Quam et al. 2001); 14. Cueva Corazón (Sánchez-Yustos et al., 2011); 15. El Castillo (Martín-Perea et al. 2023); 16. Covalejos (Martín Blanco et al., 2006; Guérin and Lahaye 2022); 17. Roca San Miguel (Peña-Monné et al. 2022); 18. Estret de Tragó (Martínez Moreno et al. 2004); 19. Vanguard Cave (Doerschner et al. 2019); 20. Las Callejuelas (Domingo et al. 2017a, b); 21. Fuente Mudarra (Santamaría et al. 2021) and Galería de las Estatuas (Demuro et al. 2019; Moreno et al. 2022; Martínez-Pillado et al. 2024); 22. Gruta da Oliveira (Zilhao et al., 2021); 23. Figueira Brava Cave (Zilhao et al. 2020)

of carcasses, Buitrago Villaplana (1992) proposed that the human groups that inhabited the upper valley of the Lozoya River during the formation of the Cueva del Camino site had no shortage of resources and that the valley provided an abundant wildlife for hunting requirements. The basis of this interpretation was the hypothesis that the main accumulation agent at Cueva del Camino was the pre-neanderthal species (Alférez et al. 1982). However, although it is now interpreted as a hyena den (see below), given the richness of the fauna recorded and the evidence of human presence, the hypothesis of Buitrago Villaplana (1992) can be defended and proposes that Neanderthals could have permanently inhabited the valley and that the meat resources were sufficient to sustain them. To test this hypothesis, the objective of this work is to evaluate the ecological conditions of the ecosystem of Cueva del Camino through the parameters of carrying capacity and available meat. The results will be compared to the ecological conditions of other past and present ecosystems, and it will be discussed whether the resources of the Cueva del Camino ecosystem were sufficient to support human groups in a stable manner.

The sites of Calvero de la Higuera in Pinilla del Valle (Madrid, Spain): Cueva del Camino

The sites of Calvero de la Higuera in Pinilla del Valle (Madrid, Spain) are significant for studying the ecological conditions in the center of the Iberian Peninsula where Neanderthals inhabited (Arsuaga et al. 2012; Álvarez-Lao et al. 2013; Moclán et al. 2018, 2021) (Fig. 1). The archaeological sites of Calvero de la Higuera were discovered in 1979 and subsequently excavated by paleontologists and archaeologists, resulting in the recovery of a substantial Pleistocene fossil record, including lithic tools and human remains that have been assigned to the Neanderthal species (Alférez et al. 1982; Alférez and Roldán Garrido 1992; Maldonado Díaz 1996; Arsuaga et al. 2010). One of the richest sites in terms of archaeological and paleontological evidence is Cueva del Camino (40°55′27″ N, −3°48′34″ E), with a great biodiversity of large mammals and microvertebrates (see below), that reflects a complex palaeoecological environment (Alférez and Roldán Garrido 1992; Arsuaga et al. 2010; Baquedano et al. 2010, 2023; Álvarez-Lao et al 2013). For this reason, Cueva del Camino represents a natural testing ground for the study of Neanderthal paleoecosystems in the center of the Iberian Peninsula and, therefore, it is of great interest to analyze the parameters of CC and TAB. In addition, this site is relevant to understanding human adaptations and evaluating regional behavioral models, including patterns of human mobility, site reoccupation, and resource exploitation over time. Since the evidence suggests that human populations consistently occupied this region, the rest of the sites of Calvero de la Higuera — the Navalmaíllo Rock Shelter, the Buena Pinta cave, the Ocelado Rock Shelter and the Des-Cubierta cave (Fig. 1C) — together with Cueva del Camino, collectively highlight the importance of the upper valley of the Lozoya River as a focal point for human activity shedding light on aspects such as subsistence strategies (hunting, processing, and food consumption) and the interplay between humans and their environments from the Middle Pleistocene to the Holocene (Arsuaga et al. 2012; Baquedano et al. 2010; 2014; Moclán et al. 2018, 2021).

Cueva del Camino was the first site of Calvero de la Higuera to be excavated and its discovery was a result of construction works aimed to build a road at the end of the Pinilla reservoir (Arsuaga et al. 2010). The campaigns of excavations have allowed to obtain one of the most complete non-Mediterranean lists of mammal fauna of the last interglacial period of the Pleistocene in the Iberian Peninsula (Baquedano et al. 2010; Álvarez-Lao et al 2013). Although the fossil record of Cueva del Camino registered a large presence of carnivores (especially hyenas), the site was initially proposed to be of anthropic origin due to the presence of lithic tools, the scarcity of carnivore coprolites and the recovery of two human molars, that were later assigned to Neanderthal species (Alférez et al. 1982; Alférez and Roldán Garrido 1992; Arsuaga et al. 2010). However, although it is considered that there were signs of sporadic human presence based on the lithic industry remains (Arsuaga et al. 2010; Baquedano et al. 2023), Cueva del Camino is currently interpreted as a hyena den based on: (i) the absence of hearths, (ii) the presence of hyena cub remains and coprolites displaced from depositional areas, (iii) accumulation of animal bones that presented tooth marks and fracture patterns that match the hyena bite as well as digested bones (Díez Fernández-Lomana 1993; Arsuaga et al. 2010, 2012). Even though the assemblage presents a mixed taphonomic origin, there is no direct evidence that humans contributed to the accumulation or modification of the faunal remains. Human activity, although notable, appears to have been limited within the taphonomic context of the site. Nevertheless, the relationship between humans and the paleoecosystem of Cueva del Camino appears to be directly related to the mobility of human groups in the area, with space use and resource availability playing a key role as limiting factors (Moclán et al. 2021).

Cueva del Camino shows a complex scenario since the cave ceiling collapsed, and its original morphology had disappeared due to the river networks, low temperatures and erosion (Alférez et al. 1982; Baquedano et al. 2014). The deposit is divided into four sectors: North, Central, Diaclasa Roja and South, being those in the north the oldest and those in the south the most recent (Pérez-González et al. 2010). The fossils are mainly concentrated in the northern sector, where seven stratigraphic layers can be

distinguished (Baquedano et al. 2014) (Fig. 1D). Layer 05, dated ~ 90.000 years by thermoluminescence (TL) in two sediment samples using the standard procedures (Pérez-González et al. 2010; Arsuaga et al. 2012) and corresponds to MIS 5c. It contains most of the macrofauna, presenting a greater biodiversity in comparison to other levels, and providing relevant information to know the paleontological, palaeoecological and paleoenvironmental conditions of Central Iberia in this period (Álvarez-Lao et al. 2013).

Although Cueva del Camino stands out for its rich paleontological record, characterized by extensive faunal assemblages and evidence of paleoecological diversity and anthropogenic activity, the Last Interglacial period in Central Iberia is also represented by several other sites of significant relevance. These sites provide valuable insights into human habitation, subsistence strategies, and environmental conditions during this time. For instance, the Navalmaíllo Rock Shelter, as previously mentioned, has yielded a variety of lithic tools and faunal remains, providing evidence of Neanderthal occupation and resource exploitation (Moclán et al. 2018, 2021). These findings suggest a warm climate with a mosaic landscape comprising woodland, open areas, and rocky environments, which would have supported diverse human activities (Moclán et al. 2021). Similarly, Cueva de los Torrejones (Tamajón, Guadalajara) provides paleoecological data for the MIS 5 period, supporting a diverse faunal assemblage (Sala et al. 2021). Another valuable contribution to understanding the conditions of MIS 5c comes from the macro and micromammal record of the HAT site (Valdetorres de Jarama, Madrid) (Álvarez-Lao et al. 2013).

The fossil record of Cueva del Camino layers shows well-preserved remains, from which fifteen large mammals (> 10 kg) could be identified, in addition to Neanderthals. Among the artiodactyls we can find: the red deer (*Cervus elaphus*), the fallow deer (*Dama dama*), the roe deer (*Capreolus capreolus*), the aurochs (Bovini cf. *Bos primigenius*), the chamois (*Rupicapra pyrenaica*) and the wild boar (*Sus scrofa*). Among the perissodactyls the horse (*Equus ferus*) and the steppe rhinoceros (*Stephanorhinus hemitoechus*) were present. There is also a large rodent, the European beaver (*Castor fiber*). The large carnivores were represented in Cueva del Camino by the spotted hyena (*Crocuta crocuta*), the wolf (*Canis lupus*), the dhole (*Cuon alpinus*), the Iberian lynx (*Lynx pardinus*), the lion (*Panthera leo*), and the brown bear (*Ursus arctos*). Small carnivores such as the fox (*Vulpes vulpes*), the wildcat (*Felis silvestris*), the European and steppe polecat (*Mustela putorius* and *Mustela eversmanni*), the weasel (*Mustela nivalis*), the otter (*Lutra lutra*) and the badger (*Meles* sp.) are also present (Arsuaga et al. 2011, 2012; Álvarez-Lao et al. 2013; Baquedano et al. 2014).

Cueva del Camino also shows a high richness of microvertebrate record with at least 51 species. Among these, 33 are small mammals, including various types of rodents such as voles (*Arvicola sapidus*, *Arvicola* cf. *terrestris*, *Chionomys nivalis*, *Microtus agrestis*, *Microtus arvalis*, *Microtus cabrerae*, *Microtus* gr. *duodecimcost*., *Microtus* aff. *malei*, *Microtus* cf. *vaufreyi*, *Myodes* cf. *glareolus* and *Pliomys coronensis*), the wood mouse (*Apodemus sylvaticus*), the hamster (*Allocricetus bursae*), the red squirrel (*Sciurus vulgaris*), the garden dormouse (*Eliomys quercinus*), and the Malayan porcupine (*Hystrix* cf. *brachyura*). Other small mammals include soricomorphs like the common shrew (*Sorex* gr. *araneus*), the Iberian desman (*Galemys pyrenaicus*) and the European mole (*Talpa europaea*), as well as erinaceids like the European hedgehog (*Erinaceus europaeus*). Chiropterans include the greater horseshoe bat (*Rhinolophus ferrumequinum*) and the lesser horseshoe bat (*Rhinolophus hipposideros*), while lagomorphs are represented by the rabbit (*Oryctolagus cuniculus*) and the hare (*Lepus* sp.). Several species of reptiles like the snake (*Natrix maura*, *Natrix natrix*, *Coronella* cf. *austriaca*, *Coronella* cf. *girondica*, *Malpolon monspessulanus,* and *Rhinechis scalaris*), the Lataste's viper (*Vipera latasti*), the ocellated lizard (*Timon lepidus*) and the Hermann's tortoise (*Testudo hermanni*), as well as amphibians like the common toad (*Bufo bufo*) and the Iberian frog (*Rana* cf. *iberica*) are also present in this faunal assemblage (Arsuaga et al. 2012). This wide variety and extensive presence of microvertebrates in the site could be a result of the Euro-Siberian and Mediterranean influence in the highlands of the upper valley of the Lozoya River, where rainfall increases and habitats diversify. In addition, the presence of micromammals is in accordance with the paleoenvironmental information provided by the association of ungulates in these environmental conditions of temperate climates (Álvarez-Lao et al 2013; Baquedano et al. 2014).

Material and methods

To reconstruct the faunal assemblage of Cueva del Camino, we first used the faunal list of species recorded in layer 05 (Arsuaga et al. 2011; Álvarez-Lao et al. 2013; Baquedano et al. 2014). For the analyses, and following Rodríguez-Gómez et al. (2020), only herbivorous mammal species weighing more than 10 kg were selected, as they would have been the main food source for hunter-gatherer populations (Owen-Smith and Mills 2008; Roebroeks 2001; Rodríguez-Gómez et al. 2014a), in addition to having higher preservation probabilities compared to micromammals (Vizcaíno, 2004; 2010; Rodríguez-Gómez et al. 2020). In this way, the following species were used for the analysis: two bovids (*Bos primigenius* and *Rupicapra pyrenaica*), three cervids (*Capreolus capreolus, Cervus elaphus,* and *Dama dama*), one suid (*Sus scrofa*), one equid (*Equus ferus*), one rhinoceros (*Stephanorhinus hemitoechus*), and one large rodent (*Castor fiber*) (Table 1 and SI 1). The faunal assemblage identified at Cueva del Camino was considered as a reliable

Table 1 Cueva del Camino faunal assemblage and life trait values used in the analyses

Species	ABM	NBM	AFB	LS	LY	AO	L
Bos primigenius	576[a]	25.57[f]	2.26[g]	1.00[e]	1.00[e]	0.50	20.00[e]
Rupicapra pyrenaica	25[b]	2.25[e]	3.75[e]	1.00[e]	1.00[e]	0.50	20.00[b]
Capreolus capreolus	31[a]	1.21[e]	2.00[e]	1.50[j]	1.00[e]	0.75	15.00[i]
Cervus elaphus	162[a]	8.26[e]	2.14[h]	1.09[e]	0.90[g]	0.49	26.80[e]
Dama dama	92[a]	4.70[e]	3.00[e]	1.00[e]	1.00[e]	0.50	25.00[e]
Sus scrofa	120[c]	0.81[e]	0.85[e]	4.52[e]	1.59[e]	3.59	10.50[k]
Equus ferus	371[d]	37.90[e]	3.92[i]	1.00[e]	1.00[e]	0.50	36.00[i]
Stephanorhinus hemitoechus	1123[a]	35.00[e]	6.70[e,g]	1.00[e]	0.30[e,g]	0.15	47.00[e]
Castor fiber	19[e]	0.50[e]	2.50[e]	2.95[e]	1.00[e]	1.48	25.00[e]

ABM; adult body mass (kg), *NBM*; neonate body mass (kg), *AFB*; age at first birth, *LS*; litter size, *LY*; litters per year, *AO*; annual female offspring, *L*; longevity (years)

[a] estimates from values in Buitrago Villaplana (1992), [b] Pérez-Barbería et al. (2010), [c] estimates from values in Alférez and Buitrago (2019), [d] estimates from values in Maldonado Díaz (1996), [e] Jones et al. (2009), [f] Rodríguez-Gómez et al. (2017c), [g] Magalhães and Costa (2009), [h] Carranza (2011), [i] Myers et al. (2023), [j] Mateos-Quesada (2011), [k] Fernández-Llario (2017)

reflection of the ecosystem composition and the taxonomic richness that inhabited the area during the sediment deposition, as it follows the criteria of Rodríguez-Gómez et al. (2017c), which considers Pleistocene ecosystems to be complete when at least 8 primary consumers and 4 secondary consumers are present.

To model prey populations, specific ecological, physical, and fertility traits have been compiled (adult body mass, neonate body mass, age of the first litter, litter size, number of litters per year and longevity) for each species, based on their modern analogues (Table 1). The use of these traits from modern analogues provides a practical approach to modeling prey populations, although it must be recognized that even in current populations there is high variability in these traits that can be influenced by factors such as ecological pressures, resource availability, and climatic conditions (see Gaillard et al. 2000). They were compiled from different databases: (i) the Enciclopedia Virtual de los Vertebrados Españoles (López and Martín, 2023) and its references, which reflect with a higher accuracy the numerical data of the species from the Iberian Peninsula; (ii) PanTHERIA, which compiles the largest number of references by species (Jones et al. 2009); (iii) AnAge: The Animal Ageing and Longevity Database (Magalhães and Costa 2009); and (iv) Animal Diversity Web (Myers et al. 2023) (Table 1). For species of extinct mammals, such as *Stephanorhinus hemitoechus*, values of current members of the Rhinocerotidae family have been used: *Ceratotherium simum*, *Diceros bicornis*, *Rhinoceros unicornis*, *Dicerorhinus sumatrensis* and *Rhinoceros sondaicus*. In the case of *Bos primigenius*, the median of the species in the subfamily Bovinae was used because their body masses are similar. Following Rodríguez-Gómez et al. (2017c), we used the median value to calculate life traits since we did not observe a correlation between the body mass and the rest of the parameters. From the fossil record of Cueva del Camino, we estimated the adult body mass of large herbivore species. 45 specimens were used to estimate the body mass of *Bos primigenius*, 15 for *Capreolus capreolus*, 204 for *Cervus elaphus*, 220 for *Dama dama*, 96 for *Sus scrofa*, and 12 for *Stephanorhinus hemitoechus* (Table 2). In the case of *Equus ferus*, we used average values of 14 dental and postcranial anatomical elements. In the absence of enough *Rupicapra* and *Castor* remains, we used body mass values from databases (Table 1). Body mass estimates were calculated using allometric equations. We used Damuth's (1990) equations for dental remains and Scott's (1990) equations for postcranial remains. The rhinoceros estimates were very low using Scott's (1990) equations because no specific equations were suitable for rhinoceroses. Therefore, we used the equations of Fortelius and Kappelman (1993) for radius and humerus. These types of equations usually have indices that allow their predictive ability to be assessed, one of which is the percentage prediction error (%PE), which indicates the percentage difference between the actual value and the value predicted by the equations. For this reason, equations with %PE values greater than 100% were discarded. When different estimates were obtained from the same specimen, each of these estimates was treated independently. The average weight of individuals was estimated in each population by weighting according to the %PE of the estimate, following Filippini et al. (2022), so that the equations with the highest predictive ability would have the highest weight. The average body mass of the individuals in the population was calculated from this average value for adult individuals. For each species, the average adult body mass (ABM) was considered taking into account both sexes and calculated as the arithmetic mean between the body mass of the male and the female. The mean neonatal body mass was used to infer the body size of individuals at different age intervals. The age of the first litter was obtained directly from the databases or was calculated as the sum of the time in which the female reaches reproductive maturity and

Table 2 Remains and numbers of fossils used to estimate the body mass of the large herbivore species from Cueva del Camino

	Bos primigenius	*Capreolus capreolus*	*Cervus elaphus*	*Dama dama*	*Sus scrofa*	*Equus ferus*	*Stephanorhinus hemitoechus*
P^1					2		
P^2	2		19	42	4	*	
P^3	1		20	45	7	*	
P^4	2		24	46	5		2
M^1	4	1	15		7	*	
M^2	4	1	23		5		
M^3	3		17		6	*	
P_2	2		2		4	*	
P_3	1	4	4		6	*	
P_4	1	2	10		7		
M_1		3	13		7	*	
M_2		3	21		9		
M_3	1	1	12		8	*	
Humeri			6	12		*	1
Radii	1		5	9		*	1
Metacarpals	6		6	33		*	4
Femurs						*	
Tibiae	7		3	14		*	
Metatarsals	10		4	19		*	4
Total	45	15	204	220	96		12

Most of the measurements are taken from the work of Buitrago Villaplana (1992), but in the case of the wild boar the values are taken from Alférez and Buitrago (2019); for the horse the values are taken from Maldonado Diaz (1996) and for the rhinoceros from Alférez and Íñigo (1990). * The mean values were used for horse remains

the gestation period. For the annual number of offspring, a 1:1 ratio of males to females at birth was assumed, considering only female individuals for population survival and mortality profiles (see Rodríguez-Gómez et al. 2022b). Therefore, the calculation of annual offspring was based on the number of litters per year, the number of offspring born in each litter, and the sex ratio, i.e. the number of total offspring divided by 2. Longevity data corresponds to wild populations, with captive data discarded. All these life history traits are a fundamental source of information and a starting point to characterize species at a biological level and delve into their population dynamics (Rodríguez-Gómez et al. 2013). These parameters will be used to obtain survival and mortality profiles, which will allow calculating CC and TAB, respectively. In this study, the approach of Rodríguez-Gómez et al. (2022a) was followed to estimate CC or prey biomass of paleocommunities and the PSEco model (Rodríguez-Gómez et al. 2024a, b) was used to estimate the amount of TAB provided by the prey community, following the procedure of Rodríguez-Gómez et al. (2013, 2014a, 2016b, 2024a). The models used in this study were chosen due to their simplicity, accessibility, and proven applicability in ecological and paleoecological studies. Their flexibility adapts to various population dynamics, and its reliability with small datasets makes it well-suited for archaeological contexts where data is often limited (see Rodríguez-Gómez et al. 2022a, b). The computational efficiency of this procedure simplifies its implementation, supporting reproducibility and enabling other researchers to apply it in similar studies (e.g., Wilson and Parker 2023).

Both for the estimation of CC and TAB is necessary to estimate the average body mass of individuals at different ages and population densities. Given that body size is one of the most relevant parameters in prey selection (Palmqvist et al. 1996; Carbone et al. 1999; Radloff and Du Toit 2004; Ercoli et al. 2014), these approaches consider the proportion of subadults, a relevant aspect for CC estimates (see Rodríguez-Gómez et al. 2022a, 2024b) or for analyses intended to estimate the exploitation of meat resources by large predators (see Rodríguez-Gómez et al. 2013, 2014a, b, 2016b, 2017a, b, c, 2020, 2022b, 2024a, b). To estimate the body masses of the prey species at different age intervals, we followed the proposal of Zullinger et al. (1984):

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

where M (t) is the mass at age t, ABM is the asymptotic body mass (i.e., the adult body mass, in g), K the growth

rate constant (days^{-1}), and I is the age at the inflection point (days). K relates to adult body mass following the equation:

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

The average mass for each age interval was estimated as the arithmetic mean of the two most extreme values within each age interval.

For estimating density values, we used the Damuth's Eq. (1981) derived for European mixed temperate forests:

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

where D is the population density (individuals/km^2), and ABM is in g.

In order to estimate CC in the Cueva del Camino paleocommunity, we used the approach of Rodríguez-Gómez et al. (2022a):

$$B = \sum_{i=1}^{n} P_i * M_i * D, i = 1, \ldots, n. \quad (4)$$

where B is the biomass of the population, P_i is the relative proportion of individuals in the population in age interval i, and overall represents the population age structure, M_i is the average body mass of the individuals of age interval i and D is the density of the population. To calculate the relative proportion of individuals of each age class (P_i), we used:

$$P_i = \frac{l_i}{\sum_{i=1}^{n} l_i}, i = 1, \ldots n, \quad (5)$$

where l_i is the proportion of individuals in the cohort who survive in class i. We obtained the l_i values for estimating P_i from survival profiles calculated by the Weibull model (see Martín-González et al. 2016, 2019):

$$S(t) = e^{(\frac{-t}{\lambda})^{k}} \quad (6)$$

This is a non-linear equation with two parameters (K and λ). This equation has an infinite number of solutions. However, if K is fixed, the value of λ_{est}(K) within the interval [0, 2] can be derived using numerical approximation methods, and thus it is possible to obtain stable and stationary survival profiles. Once the survival profiles have been calculated, we obtain the distribution of individuals by age groups in each population (Rodríguez-Gómez, 2022a, b). This enables us to estimate the age structure, which reflects the proportion of individuals for each age group. The proportion of individuals and body mass per age interval, together with the population density, provides the biomass that each age interval contributes to the total biomass of the population. CC of the paleoecosystem is calculated by summing the biomass of all species.

In the case of TAB, we used PSEco (see Rodríguez-Gómez et al. 2024a), which uses the mortality profiles (also calculated by the Weibull model) of the large herbivore species of a community to estimate the number of individuals that could die annually without causing their populations to collapse (see Rodríguez-Gómez et al. 2013; Martín-González et al. 2016, 2019). PSEco uses faunal lists, life history trait values (Table 1) and densities of prey species in the paleoecosystems to provide estimates of the amount of prey biomass that can be extracted annually from a paleoecosystem. We used an equation similar to Eq. 4, substituting l_i for the proportion of deaths between ages (d_i) (d_x=l_x—l_{x+1}):

$$OutputBiomass = \sum_{i=1}^{n} d_i * M_i * D, i = 1, \ldots, n, \quad (7)$$

The sum of the output biomasses of all the species in the community yields what is referred to as the Total Output Biomass (TBO) in Rodríguez-Gómez et al. (2014a). Based on TBO, PSEco applies a "wastage factor" that estimates the percentage of biomass not used by the secondary consumers (e.g., skin, horns, and bones) (see Rodríguez-Gómez et al. 2013, 2014a, b, 2020, 2024a, b). This results in the biomass available to the secondary consumers (in kg/km^2*year and kcal/km^2*year), which is referred to in the PSEco model as TAB (Total Available Biomass) (Rodríguez-Gómez et al. 2014a). Given that the Weibull model provides infinite mortality profiles, PSEco only considers the extreme values corresponding to maximum and minimum subadult mortality (Martín-González et al. 2016, 2019). In this way, TAB-min is the available biomass corresponding to maximum subadult mortality (and minimum adult mortality), while TAB-MAX refers to the opposite situation.

For both CC and TAB, the biomass was divided 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. This allows consideration of the role of body size as the most relevant factor in prey selection (Palmqvist et al. 1996; Carbone et al. 1999; Radloff and Du Toit 2004; Ercoli et al. 2014) and the contribution of each population to the different body size classes, and in turn comparison of values and patterns between CC and TAB.

Based on the results of CC and TAB, the relative percentage of each family in each index was estimated. The species were grouped into families to facilitate and simplify the analyses. For the fossil record, the Minimum Number of Individuals (MNI) and Number of Identified Specimens (NISP) values were used to estimate relative percentages (Arsuaga et al. 2012). The tendency of MNIs to underestimate common species and overestimate rare species when considering MNI was noted (see Arribas and Palmqvist 1998). However, this type of approach allows taking into account the presence of some species represented by scarce fossil or ichnofossil remains in fossil records (see Rodríguez-Gómez et al. 2024b). Comparisons between the relative proportions of families in the CC, TAB and fossil record were performed using the χ^2 test, as in Rodríguez-Gómez et al. (2024b).

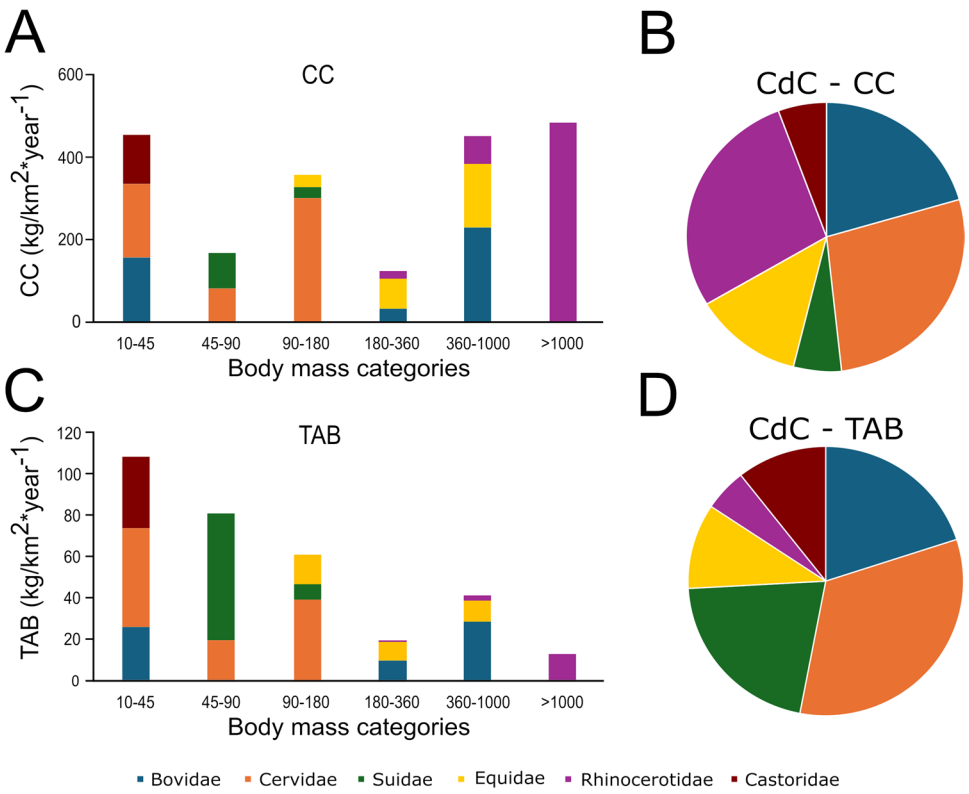

Fig. 2 Carrying capacity (CC) (**A**, **B**) and total available biomass (TAB) (**C**, **D**) values distributed among six body mass categories (**A** and **C**, respectively) (in kg/km^2*year.$^{-1}$) and their relative percentages (**B** and **D**, respectively). The colors represented in the histograms and cheese diagrams correspond to the different species families of Cueva del Camino (CdC)

Results

Carrying capacity (CC) and Total Available Biomass (TAB) values were obtained for the mammal communities of Cueva del Camino (CdC) and distributed among the six body mass categories considered in the study (see Fig. 2). It can be seen that the total CC values, including all categories, reach an average sum of 2037.40 kg/km^2*year^{-1} (Tables 3 and 4). Class 6 (> 1000 kg) is the one that concentrates the most biomass compared to the other classes, representing 23.8% of the total. Classes 1 (10–45 kg) and 5 (360–1000 kg) show similar values with percentages close to 22%. Classes 2 (45–90 kg) and 4 (180–360 kg) are much lower than the others, with percentages of 8.2% and 6.1%, respectively, resulting in a discontinuous pattern between CC values among the different body mass categories (Fig. 2A). As can be seen in Fig. 2B, the bovid, cervid, and rhinoceros families stand out for their contribution to the Cueva del Camino carrying capacity.

According to the TAB values, the results give a total sum of 324.15 kg (Tables 3 and 4). In this case, the body mass categories show a different distribution than the CC pattern, with a tendency to have less biomass in the higher body mass classes, with the exception of class 5 (360–1000 kg) (Fig. 2C). Class 1 accounts for 33.37% of the total, concentrating slightly more than a third of the TAB. Classes 4 (180–360 kg) and 6 (> 1000 kg) have the lowest percentages of TAB, 6.10 and 4.04%, respectively. As can be seen in Fig. 2D, the contribution of the species of the families bovidae, cervidae and suidae to the TAB stands out.

With respect to the total CC values, TAB represents a 15.91% (Table 4), which is the available biomass percentage for secondary consumers that would have to leave the ecosystem annually to keep the community in a stable and stationary state. In other words, the amount of meat available to secondary consumers represents almost one-sixth of the CC that the ecosystem can sustain. If we consider the relationship between the different categories of body mass, the percentages of TAB with respect to CC are as follows: in Class 1, TAB represents 23.94% of CC; in Class 2, 48.22%; in Class 3, 17.02%; in Class 4, 15.97%; in Class 5, 9.15%; and in Class 6, 2.70%. In this case, the highest percentages of TAB in relation to CC are found in the first three classes and the lowest in the last three. Of note is the ratio in Class 2, where the reproductive nature of the wild boar allows it to be exploited more intensively.

When examining the different species represented, it is important to keep in mind that they can be divided into more than one class, since age structures are used and therefore the distribution of adult and subadult individuals can be observed (Table 3, Fig. 2A and C). These age distributions, together with the density values of each species and their reproductive rates, are parameters that are indirectly reflected in the proportions of both CC and TAB values. Out of a total of 9 mammal species, the first and third classes

Table 3 CC and TAB values (in kg/km^2*year-1) by body mass categories in all species analyzed

CC	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Total
Bos primigenius	0	0	0	32	231	0	263
Rupicapra pyrenaica	157	0	0	0	0	0	157
Capreolus capreolus	154	0	0	0	0	0	154
Cervus elaphus	0	29	184	0	0	0	213
Dama dama	25	53	118	0	0	0	196
Sus scrofa	0	86	27	0	0	0	112
Equus ferus	0	0	30	74	152	0	257
Stephanorhinus hemitoechus	0	0	0	17	68	484	569
Castor fiber	116	0	0	0	0	0	116
Total	452	167	359	124	451	484	2037
TAB	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Total
Bos primigenius	0	0	0	10	29	0	39
Rupicapra pyrenaica	26	0	0	0	0	0	26
Capreolus capreolus	38	0	0	0	0	0	38
Cervus elaphus	0	12	25	0	0	0	37
Dama dama	10	8	14	0	0	0	32
Sus scrofa	0	61	8	0	0	0	68
Equus ferus	0	0	14	9	10	0	33
Stephanorhinus hemitoechus	0	0	0	1	2	13	17
Castor fiber	34	0	0	0	0	0	34
Total	108	81	61	20	41	13	324

The body mass categories are 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) and Class 6 (> 1000 kg)

contain the most, with 4 species each. The second, fourth, and fifth categories contain 3 species, and the sixth category contains only one. *D. dama*, *E. ferus* and *S. hemitoechus* are the most abundant species in all body mass categories, being present in three (see Table 3). Conversely, *C. capreolus*, *C. fiber* and *R. pyrenaica* are present only in Class 1.

The species with the highest amount of biomass in the total CC values are *S. hemitoechus* with 28.33% (569.47 kg), *B. primigenius* with 12.85% (263.16 kg) and *E. ferus* with 12.53% (256.60 kg) (Table 3). The remaining species represent the following percentages: *C. elaphus* a 10.45% (212.82 kg), *D. dama* a 9.62% (196.03 kg), *R. pyrenaica* a 7.72% (157.19 kg), *C. capreolus* a 7.54% (153.66 kg), *C. fiber* a 5.70% (116.10 kg) and *S. scrofa* a 5.51% (112.35 kg). The species with the highest amount of biomass in the TAB total values is *S. scrofa* with a 21.10% (68.41 kg), while the rest of the species represent the following percentages: *B. primigenius* a 11.91% (38.61 kg), *C. capreolus* a 11.70% (37.91 kg), *C. elaphus* a 11.35% (36.78 kg), *C. fiber* a 10.58% (34. 30 kg), *E. ferus* a 10.22% (33.11 kg), *D. dama* a 9.96% (32.28 kg), *R. pyrenaica* a 8.07% (26.15 kg), and *S. hemitoechus* a 5.12% (16.59 kg). All in all, these percentages indicate that the rhinoceros dominates the total CC values compared to other species, followed by the aurochs and the horse. The lowest values are those of roe deer, beaver and wild boar. In the case of TAB, wild boar is the species with the highest values, while the rest of the species have similar values, ranging from about 5 to 12%.

Discussion

The analyses carried out in this study aimed to inform about the availability of meat in the Cueva del Camino paleoecosystem. These provide information about the abundance of prey that inhabited the upper valley of the Lozoya River, which would likely have affected the dispersal patterns of both human groups and carnivore species (Arribas and Palmqvist 1999; Palombo 2013, 2016). The results indicate that both the CC and TAB distributions were not homogeneous but vary along the six body mass classes (Table 3 and Fig. 2). The CC is concentrated in the first and last two prey body mass classes, indicating that the contribution comes mainly from small sized species with high reproductive rates, such as *C. fiber*, *C. capreolus* or *R. pyrenaica*, but also from large species with low reproductive rates, such as *B. primigenius*, *E. ferus* and *S. hemitoechus*. Smaller species tend to have lower survival rates because they are more vulnerable prey (in addition to having a shorter life span) than larger species. In population dynamics, this would be compensated with a higher reproductive rate and a higher number of offspring per litter, reaching sexual maturity at an

Table 4 CC (in kg/km^2*year-1), TAB (in kg/km^2*year-1) and relation (TAB/CC) for CdC (Cueva del Camino), sites of Atapuerca (Trinchera Elefante (TE), Trinchera Dolina (TD) and Galería (G)) and of Orce (Venta Micena (VM) and Barranco León/Fuente Nueva-3 (BL/FN3))

Faunal assemblages	CC	TAB	Relation (TAB/CC*100)(%)
BL/FN3	3535.26[a]	387.49[a]	10.96[a]
VM	3813.39[a]	468.21[a]	12.28[a]
TE9	1842.21[b]	-	-
TE14	1680.27[b]	-	-
TE19a-e	1766.00[b]	-	-
TD3-TD4	1987.31[a]	287.43[a]	14.46[a]
TD6-3	1286.59[b]	-	-
TD6 1–2	2595.37[a]	346.12[a]	13.34[a]
TD7	1175.25[b]	-	-
TD8	2618.12[a]	326.50[a]	12.47[a]
TD10-3	1478.82[b]	-	-
TD10-2	1954.77[b]	-	-
TD10-1	1966.97[a]	236.90[a]	12.04[a]
Glla	1948.35[b]	-	-
Gllb	2237.80[a]	311.23[a]	13.91[a]
GIII	2237.80[a]	311.23[a]	13.91[a]
CdC	2037.40[c]	324.15[c]	15.91[c]

[a] values from Rodríguez-Gómez et al. (2024a), [b] values from Rodríguez-Gómez et al. (2022a), [c] this study

earlier period (Jones et al. 2009; Magalhães and Costa 2009; Myers et al. 2023). Conversely, larger species have higher survival rates because their weight makes them harder for predators to catch and because the young are protected by large adults. They also have longer reproductive intervals and typically have only one offspring per litter, in addition to reaching sexual maturity at a later period (Derrickson 1992; Jones et al. 2009; Magalhães and Costa 2009; Myers et al. 2023). Lower values of CC are concentrated in intermediate classes representing medium-sized species, such as *D. dama*, *C. elaphus* and *S. scrofa* (Table 3 and Fig. 2). Medium-sized species could be easily selected by most secondary consumers and, while the cervids have slow reproductive rates and few offspring, the wild boar has shorter reproductive intervals and many offspring, although with a shorter longevity than *D. dama* and *C. elaphus* (Jones et al. 2009). Based on this distribution, we can affirm that the paleoecosystem of Cueva del Camino was composed of a greater amount of biomass derived from small and large prey, especially from the larger ones (*B. primigenius*, *E. ferus* and *S. hemitoechus*), in which the sum of their biomass exceeds 50% of CC (Table 3 and Fig. 2). Although the largest biomass contributions belong to larger species, it should be kept in mind that the larger the body mass, the lower the density of the species and, thus, the less recurrent meat resource compared to species with smaller body mass. The latter would provide smaller amounts of meat per individual, but with more frequent availability (Rodríguez-Gómez et al. 2024a).

The distribution of the TAB, on the other hand, shows that almost one third of the total value of available meat is concentrated in the first class and the other two thirds are distributed among the remaining classes (Table 3 and Fig. 2). Class 1 represents most of the TAB, but it should be noted that in the case of small species, all age groups of their populations are concentrated in the same class (10–45 kg), i.e. adult and subadult individuals. Conversely, the age groups of larger species are distributed in more than one body mass class and therefore represent a smaller percentage in each of them. Some of the species included in Class 1 provide the highest values of TAB: *C. fiber* and *C. capreolus*. This suggests that those species with higher values of available meat would be the most likely to be selected by most secondary consumers due to their smaller body mass. Species with larger body sizes showed greater amounts of available meat concentrated in the larger body size categories. This could be due to a greater number of individuals reaching an advanced age, which is consistent with the vital characteristics of this type of species; they are less likely to be hunted when young (Martín-González et al. 2019). In conclusion, most of the CC of the Cueva del Camino ecosystem is represented by larger species: *S. hemitoechus*, *E. ferus* and, *B. primigenius*, while the highest amount of TAB is represented to a greater extent, by species of smaller sizes: *S. scrofa*, *C. fiber* and *C. capreolus* (Table 3 and Fig. 2).

In order to contextualize the abundance and distribution of the Cueva del Camino resources, their values will be compared with other faunal assemblages of past and present ecosystems. Regarding past ecosystems, the archaeological and paleontological sites of Orce (Granada) and Sierra de Atapuerca (Burgos) in the Iberian Peninsula (Fig. 1A and Table 4) have been considered, where the methodological approaches for estimating CC and TAB have previously been applied, as in the present work (see Rodríguez-Gómez et al. 2024a). The sites of Orce, Venta Micena (VM), Barranco León and Fuente Nueva-3, are dated in the Early Pleistocene (Duval et al. 2012; Toro-Moyano et al. 2013). According to the sites of the Sierra de Atapuerca, different levels that belong to three sites were used: Sima del Elefante (Trinchera Elefante, TE), which extends from the Early to the Late Pleistocene, Galería (G), that extends from the Middle to the Late Pleistocene, and Gran Dolina (Trinchera Dolina, TD), that extends from the Early to the Middle Pleistocene (Bermúdez de Castro et al. 2013; Benito-Calvo et al. 2017; Bógalo et al. 2021; Duval et al. 2022; Rodríguez et al. 2011; Rodríguez-Gómez et al. 2022a). These sites are interesting to compare because they are very relevant to the study of early human settlements in Western Europe in the Early

Pleistocene, as well as to the debate about human dispersal routes and technological-cultural developments, and because they record large faunal assemblages (Bermúdez de Castro et al. 2013; Carotenuto et al. 2016; Rodríguez-Gómez et al. 2016b; 2017a). The CC and TAB values of Sierra de Atapuerca and Orce were extracted from Rodríguez-Gómez et al. (2022a, 2024a) and the relationship between both parameters was evaluated from the average of the minimum and maximum values of CC and TAB (Table 4). In general, it can be observed (Table 4) that Cueva del Camino shows a CC value (2037.40 kg/km^2*year^{-1}) higher than the paleocommunities of the Sierra de Atapuerca sites, similar to TD3-TD4 (1987.31 kg/km^2*year^{-1}) and lower than the paleocommunities of Venta Micena, Fuente Nueva 3 and Barranco León, TD6 1-2, TD8, Gllb and GIII. According to the TAB values, Cueva del Camino (324.15 kg/km^2*year^{-1}) shows a value similar to TD8 (326.50 kg/km^2*year^{-1}) and is exceeded by TD6 1–2, Venta Micena, Fuente Nueva 3, and Barrando León (Table 4). All in all, it can be observed that Cueva del Camino's values in CC and TAB are not particularly outstanding. However, it presents the highest values in terms of the ratio between the two parameters. This ratio refers to the percentage of the total biomass that would have to be renewed annually in the ecosystem to maintain stable and stationary conditions, so higher numbers would indicate a higher renewal rate, suggesting a more accelerated reproductive rate of the species that composed the Cueva del Camino community. Considering that the faster reproductive rates belong to smaller species, it can be said that Cueva del Camino would have had fewer megaherbivores than the Orce and Atapuerca ecosystems. In fact, the only megaherbivore we find in Cueva del Camino is the rhinoceros, as in other sites in Calvero de la Higuera, such as the Navalmaíllo Rock Shelter and the Des-Cubierta cave (Arsuaga et al. 2012; Moclán et al. 2021; Baquedano et al. 2023). Atapuerca and Orce also record mammoths and hippopotami (Rodríguez et al. 2011; Rodríguez-Gómez et al. 2024b). Differences in species composition between ecosystems are generally related to climatic conditions (water availability, temperature and solar radiation). The greater the increase in these conditions, the greater the primary production (Churkina and Running 1998; Nemani et al. 2003), which favors the increase in prey biomass (Rodríguez-Gómez et al. 2022a). In this case, the high CC values of the Orce paleocommunities compared to the Atapuerca and Cueva del Camino ones would be due to the favorable geochemical conditions of the Guadix-Baza basin, which would have allowed a greater development of megaherbivores (Rodríguez-Gómez et al. 2016b, 2017a, 2022a; García-Aguilar et al. 2024). The climatic conditions of the faunal assemblage of Cueva del Camino in the upper valley of the Lozoya River would be similar to those of today (Álvarez-Lao et al. 2013) and not as favorable as those found at the Orce sites in the Early Pleistocene (García-Aguilar et al. 2024). However, it should be noted that the results obtained in this work are the result of modeling the faunal assemblage of the Cueva del Camino record, which is interpreted as a hyena den with sporadic human presence (Díez Fernández-Lomana 1993; Arsuaga et al. 2010). The access of hyenas to the megafauna would have been limited, probably because they consumed this fauna mainly as scavengers, so the record of Cueva del Camino could be biased in this sense. This could affect our results for the CC and TAB, which may support a larger number of humans and carnivores (see below). To try to avoid this type of bias, this analysis followed the criteria of Rodríguez-Gómez et al. (2017c) to consider faunal records close to the full composition of large mammals (> 10 kg) in European Pleistocene ecosystems (see Material and Methods section).

For comparison with current ecosystems, we used as a reference an assemblage of protected natural parks from 23 African regions from the supplementary material of Hatton et al. (2015). We selected these assemblages because they provide carrying capacity values with which to compare the results for Cueva del Camino, and because globally these assemblages reach stability conditions similar to those obtained from the approximations used in this study (see Rodríguez-Gómez et al. 2024a). All these ecosystems are located in Kenya, Namibia, Zimbabwe, South Africa, Tanzania, Uganda, and Botswana. They cover a large area and have a high availability of water resources that support the communities of primary and secondary consumers. The diversity of secondary consumers between Cueva del Camino and these African parks is different, although they have some species in common (the lion and the spotted hyena). Taking the CC values of all the African parks together, the average is 2507 kg, which exceeds that of Cueva del Camino by slightly less than 500 kg. Observing the CC values of each ecosystem separately, it can be noted that Cueva del Camino (2037 kg/km^2*year^{-1}) is more similar to those of the Serengeti National Park (specifically the 1971 and 1993 censuses, with 2020 and 2000 kg/km^2*year^{-1}, respectively) and the Selous Game Reserve (with 2079 km^2*year^{-1}), both in Tanzania.

In the work of Álvarez-Lao et al. (2013), values of Minimum Number of Individuals (MNI) and Number of Identified Specimens (NISP) of large mammal species (excluding beavers) from Cueva del Camino are presented (Table SI 1). According to the relative percentages by families, no significant differences were observed between MNI and NISP values ($\chi^2 = 4.4695$; $p = 0.34618$). The MNI and NISP values mainly show a bias towards cervids (71 and 83%, respectively), especially fallow deer and red deer (see Fig. 3A). The percentages of roe deer and chamois are low and are slightly higher for larger species, such as horses, aurochs or rhinoceros (Arsuaga et al. 2012, Fig. 8). These MNI and NISP values are very different from those estimated for CC

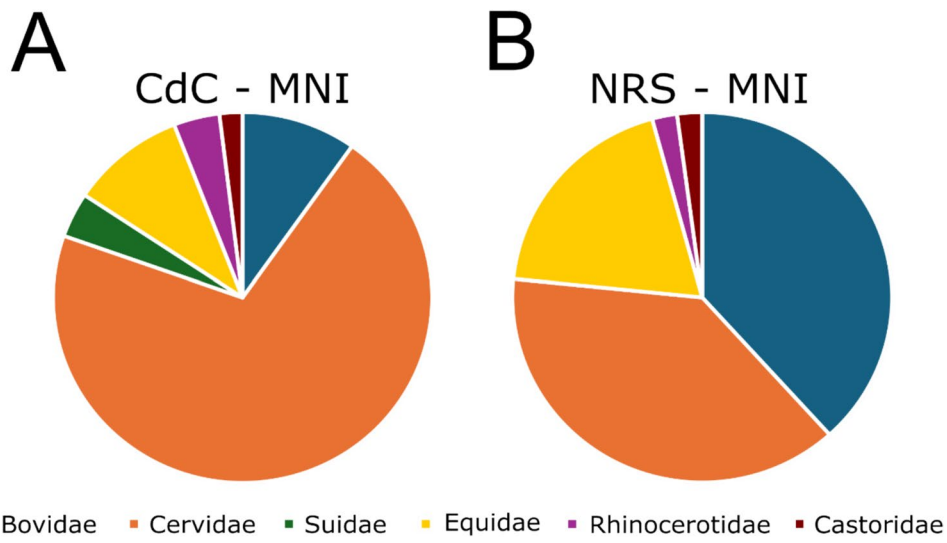

Fig. 3 Relative percentage of different families present in Cueva del Camino (CdC) and Navalmaíllo Rock Shelter (NRS) according to the Minimum Number of Individuals (MNI), following values from Arsuaga et al. (2012) and Monclán et al. (2021)

and TAB and show significant differences between them. The main difference is the percentage of cervids, which ranges from 29.28% to 36.91% in the case of CC and TAB. On the same promontory of Calvero de la Higuera is the Navalmaíllo Rock Shelter site (40º55′24″ N, −3º48′31″ E) (dated at around 70 ka BP years ago by thermoluminescence (Pérez-González et al. 2010)), which is interpreted as a Neanderthal hunting camp (Moclán et al. 2021). According to MNI values (Table SI 2), this site shows a fossil record with a greater representativeness of cervid remains (38.30%) and bovids (38.30%) compared to larger species such as horses (19.15%) or rhinoceros (2.13%) (Fig. 3B). Without taking into account the biomass of suids, that have not been found in the Navalmaíllo Rock Shelter, the cervids of Cueva del Camino represent a 27.69% in CC and a 41.83% in TAB, while bovids represent a 20.69% in CC and a 25.32% in TAB. The rhinoceros and the horse of Cueva del Camino represent a 28.03% and a 12.63% respectively in CC and a 6.49% and 12.95% in TAB. When comparing the relative percentages of these families between the MNI values of the Navalmaíllo Rock Shelter and our results in Cueva del Camino, significant differences are found with the values of CC ($\chi^2 = 31.11$; $p = <0.0001$) but not with those of TAB ($\chi^2 = 5.4716$; $p = 0.14035$). With these results, it can be proposed that the hunting activity of the Neanderthals of the Navalmaíllo Rock Shelter may be correlated with the meat resources available in the ecosystem and the record from Cueva del Camino with a specialization in the consumption of deer by spotted hyenas.

After considering the prey biomass and available resources that the Cueva del Camino ecosystem had in its respective context, we could introduce the question of how the competition between secondary consumers would have been based on their preferences by body mass categories. It must be noted that, as stated by Rodríguez-Gómez et al. (2013, 2014a, 2016a) and as can be inferred from the results, the accessibility of biomass by predators varies according to these preferences, but also according to the subsistence strategies and prey selection of other carnivores. The body size of primary consumers is an important factor in prey selection and hunting (Palmqvist et al. 1996; Carbone et al. 1999; Radloff and Du Toit 2004; Ercoli et al. 2014). It must be considered that smaller individuals would be the preferred prey of most carnivores and humans. In addition, when there is a coexistence between predators that have the same prey preferences, the intensity of the competition would be subject to the abundance of the selected species (Rodríguez-Gómez et al. 2016a). Thus, the consumption profile of carnivores and the distribution of prey in body size categories would be important factors concerning the understanding of the intensity of competition. The Cueva del Camino carnivorous species that could have had greater or lesser access to the prey considered in this study are: *Crocuta crocuta*, *Canis lupus*, *Cuon alpinus, Lynx pardinus*, *Panthera leo*, *Ursus arctos*, and *Homo neanderthalensis*. Based on the preferences by body mass categories given in Rodríguez-Gómez et al. (2017c), it can be stated that smaller carnivores such as the dhole or the lynx could hunt mainly adult and subadult individuals of wild boar, deer, beaver, and chamois. Large carnivores such as the wolf, lion or hyena would also be able to hunt small prey, but would focus primarily on larger prey such as adult fallow deer, subadult individuals of aurochs, horses or rhinoceros (from 45 to 360 kg). Human groups would have concentrated on a wide range of prey (from 10 to 180 kg), especially on small to medium-sized species, although this does not mean that they would not have had access to the largest (Rodríguez-Gómez et al. 2017c). The bear has a scavenger consumption profile without specific prey size preferences. The least vulnerable individuals in the ecosystem would have been adults

of *S. hemitoechus*, although individuals of this species could have been consumed to a lesser extent by the bear, hyena, lion, and humans, mainly as carrion. Thus, small species and young individuals of large species that are included in the first body mass class would be key prey for the subsistence of secondary consumers. The relationship in prey preferences shows that it is very likely that there was a high level of competition for resources in Cueva del Camino, which would have depended on the abundance of small prey, and that *H. neanderthalensis* would have competed with both medium and large carnivores. The lion and the hyena are the carnivore species that would have had a consumption profile more similar to that of humans and, therefore, more competition with them (Rodríguez-Gómez et al. 2017c).

Another issue we can introduce is how human groups would have had access to this resource. While some authors have suggested that human lineages during the early Pleistocene would have relied heavily on other predators for access to meat (Martínez-Navarro and Palmqvist 1996; Arribas and Palmqvist 1999; Palmqvist et al. 2011), and therefore would have been relatively independent of competitive networks, from the Middle Pleistocene on, it is proposed that subsistence strategies would have focused on an active stance through direct hunting (Richards et al. 2000; Bocherens et al. 2005; Hublin and Richards 2009; Richards and Trinkaus 2009; Churchill 2014; Smith 2015; Rendu et al. 2019, 2023; Marín-Arroyo and Sanz-Royo 2022), causing a change in the pattern of competition levels (Rodríguez-Gómez et al. 2017b, c). Furthermore, from the Middle Pleistocene on, a massive use of these activities is registered in Europe. Hunting can be associated with periods of higher competitive intensity from its earliest moments (Early Pleistocene) (Scott and Gilbert 2009; Barsky and De Lumley 2010; Moncel 2010; 2013). Nevertheless, alternative subsistence strategies such as the scavenging habits mentioned above cannot be excluded. However, hunting would have been the preferred strategy of the human groups of the upper valley of the Lozoya River (Moclán et al. 2021).

To know whether the resources from the area would have been sufficient to sustain the Neanderthal populations, human densities could be estimated from the predator biomass obtained from the Hatton et al. (2015) equation (see below Eq. 8). The study by Hatton et al. (2015) proposes a relationship between prey biomass and predator biomass:

$$y = 0.094^{*}x^{0.73}, \tag{8}$$

where y is the predator biomass and x is the prey biomass. From this equation, the predator biomass (carnivores and humans) that could be supported by the prey biomass of Cueva del Camino can be calculated. Thus, an average prey biomass or carrying capacity (CC) of Cueva del Camino of 2037.40 kg/km^2*year^{-1} (with a range of 1810.69 and 2085.82 kg/km^2*year^{-1}), would correspond to an average predator biomass of 24.48 kg/km^2*year^{-1} (with a range of 22.46 and 24.90 kg/km^2*year^{-1}). Comparing this value with those observed in African ecosystems with closer values of CC, similarities can be seen both with the Serengeti National Park (20.25 kg/km^2*year^{-1}) and with the Selous Game Reserve (31.64 kg/km^2*year^{-1}). These values suggest that the Cueva del Camino ecosystem may have had prey biomass and prey-predator biomass ratios similar to those currently observed in Serengeti National Park (1971). However, it should be noted that the CC calculations in Hatton et al. (2015) are not fully comparable with those of the present study, since the African ecosystem analysis consider prey between 5 and 500 kg and for Cueva del Camino it was considered prey from 10 to > 1000 kg. From the predator biomass, an approach to estimate Neanderthal density from relative values of population biomass was used. From the density and body mass values, a relative distribution of biomass for each species was obtained. Body mass values for carnivores were compiled from Rodríguez-Gómez et al. (2017c), and for Neanderthal groups, values were provided by Will et al (2017), which is 71 kg. From these body mass values the densities can be estimated using the allometric equation of Damuth (1993):

$$\log(D) = -0.64^{*}\log(m) + 2.23, \tag{9}$$

where D is the density of individuals per km^2 and m is the body mass (grams). In the case of humans, a density of 0.25 ind/km^2 was used, which is the average observed in modern hunter-gatherer populations (Marlowe 2005). Considering the total biomass of secondary consumers, Neanderthals would represent a 17% of the total, and if this percentage is applied to the predator biomass obtained by CC, i.e., 24.57 kg/km^2*year^{-1}, the Neanderthal biomass would be of 5.69 kg/km^2*year^{-1}. If this value is divided by the body mass of a Neanderthal (71 kg), an average density of 0.079 ind/km^2 (between 0.072–0.080 ind/km^2) can be obtained. Considering the surface of the upper valley of the Lozoya River surface (434.58 km^2) (Karampaglidis 2015) (Fig. 1B) with the density values, an average population size of approximately 34 individuals (between 31 and 35 individuals) in the area can be obtained. Comparing these density values and population size with the ones in the study by Marlowe (2005), that includes 478 samples of modern hunter-gatherer groups from different parts of the world, the following information can be obtained: the Neanderthal population density of the upper valley of the Lozoya River is low in comparison to the average density values of the hunter-gatherer groups (0.25 ind/km^2), although the differences in the median values (0.11 ind/km^2) are reduced. On the other hand, the population size is also below the values of the average population of hunter-gatherers (48.17 individuals), but above the

median values (29.50). If the percentiles are evaluated, it can be seen that the Neanderthal density is placed in the 44th percentile and the population size is in the 60th percentile in relation to the hunter-gatherer groups. This allows to say that the Neanderthal density and population size at Cueva del Camino would not have been far from the median values for modern hunter-gatherer groups. However, it should be considered that the procedure for estimating human density does not take into account parameters such as the type of diet of each secondary consumer, prey preferences, subsistence strategies and the level of competition for meat. For this reason, it would be necessary to deepen into this direction, using methodologies that take into account predator–prey relationships and competition levels for meat resources, such as those used in Rodríguez-Gómez et al. (2013, 2014a, b, 2016a, b, 2024a). Due to the complexity of these approaches to account for the different parameters, and the fact that the present study focused on CC and TAB, a simpler but innovative approach was chosen. It is hoped that in a future study, it will be possible to compare the results of this work with those obtained using more complex models. Furthermore, as previously mentioned, it is also crucial to highlight the need for detailed taphonomic analyses to refine the understanding of faunal assemblages and their palaeoecological implications, as these processes can significantly influence demographic estimates.

The CC and TAB values estimated in this study are useful tools to approximate the ecological conditions of the ecosystem and the prey populations that inhabit it. The different age groups give a more precise level of detail about the composition of the communities. However, the parameters evaluated in this study did not take into account the meat available from the micromammal species and, therefore, the resource availability would have been more diversified than what has been considered. On the other hand, it cannot be assumed that the distribution of resources was uniform in the valley, which would reduce the possibilities of exploitation and the estimates of meat available. For all these reasons, it would be interesting to study the trophic relationships, considering consumption preferences and nutritional requirements, in order to obtain more precise approximations of the sustainability conditions of the Neanderthal groups in the upper valley of the Lozoya River. It would also be useful to carry out these analyses on a larger number of faunal assemblages to evaluate in depth the palaeoecological conditions under which humans lived during the Late Pleistocene in the Iberian Peninsula.

Conclusions

In both present and past ecosystems, carrying capacity (CC) and total available biomass (TAB) are relevant tools for evaluating ecological conditions. In this study, estimates of CC and TAB were used to evaluate the conditions under which the Neanderthal groups of Cueva del Camino evolved. The results show that there was a predominance of extreme body masses in the CC of the ecosystem (very small and very large), and the least amount of biomass came from intermediate body masses. In terms of TAB, the pattern is somewhat different, being more abundant in small sizes and less abundant in large sizes. The Cueva del Camino ecosystem also reflects similar conditions to some sites in the Sierra de Atapuerca, such as Gran Dolina and Galería. Concerning current ecosystems, Cueva del Camino shows CC similarities to the Serengeti National Park. From density estimates (ind/km^2) and population size, it is observed that Cueva del Camino closely resembles populations of contemporary hunter-gatherer groups. These approximations led to the conclusion that the ecosystem conditions of Cueva del Camino may have been sufficient to support a Neanderthal group of approximately 34 individuals in the upper valley of the Lozoya River.

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Data availability Data are provided in the manuscript and supplementary materials.

Declarations

Competing interests The authors declare no competing interests.

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