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Palaeoecology of the Southern chamois from Valdegoba Cave (Burgos, Spain) and its exploitation by the Neanderthals

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The Southern chamois (*Rupicapra pyrenaica*) is a small-sized bovid that currently inhabits the Cantabrian Mountain Range, the Pyrenees, and the Central Apennine Mountains. This species was exploited as a resource by Palaeolithic human groups of the northern region of the Iberian Peninsula, standing out in the record of the Cave of Valdegoba. The fossil record of this site has provided plenty of evidence of Neanderthal activity. According to taphonomic analyses, Neanderthals had primary access to prey and chamois was the most consumed species. Analysis of Valdegoba's Southern chamois allows consideration of: (1), the age structure and the dynamics of the population; (2) the palaeobiological characteristics of this population (e.g. mortality rate by age intervals, growth rate or body mass); (3) comparison of the population dynamics of Valdegoba's chamois with that of present-day populations of different species (*R. rupicapra*, *R. pyrenaica*); and (4) exploitation of the chamois by Neanderthals. We focussed on methodological aspects of population structure and mortality profiles using life tables with vital statistics, Leslie-Lewis matrices and ternary diagrams starting from tooth eruption and wear, whereas mass estimates were obtained from the postcranial bones. Cohort structures from extant Southern, Alpine and New Zealand chamois populations were compared to Valdegoba's chamois to better understand the paleoenvironmental context of this fossil species. In addition, we calculated the amount of meat available to the Neanderthals and the extent of their range and its population implications. Our results show that the age structure of Valdegoba chamois reflects a very similar structure and ecological features to present-day populations. Moreover, modelling the age structure of Valdegoba population shows that Neanderthals could have exploited the Southern chamois without leading to the collapse of the population. Based on the results of energetic inputs related to the percentage of chamois in Valdegoba, where we estimate that a Neanderthal group would have had to exploit at least an area of between 61 and 99 km^2 to cover their energetic requirements. ☐ *Paleoecology,* Rupicapra pyrenaica, *life tables, body mass, sustainability, Neandertal, human ecology.*

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The Southern chamois, *Rupicapra pyrenaica*, comprises 58% of the herbivorous remains in Valdegoba cave deposit of Burgos, Spain, representing more than 100 individuals and the main source of meat for the Neanderthals that inhabited the cave (Arceredillo 2015; Díez 2006; Díez *et al.* 1989; Díez Fernández-Lomana *et al.* 2014; Quam *et al.* 2001). This study aims to exhaustively describe the population dynamics and the available biomass of the chamois of Valdegoba, using current knowledge of different modern populations of *Rupicapra* in order to infer how the Neanderthal groups may have exploited this species during the Middle Palaeolithic. For this purpose, we combine different methodological tools such as mortality profiles and ternary diagrams, life tables, Leslie-Lewis matrices, and allometric equations to estimate body masses, providing an innovative and original approach to complement our view of Middle Palaeolithic human populations and their subsistence strategies. However, it is necessary to bear in mind that applying this approach requires a fossil record with a high representation of individuals in the different age intervals of the mortality profiles catastrophic mortality profiles to be able to infer the ecological characteristics of the population; as well as remains that allow estimating the body masses of the adult individuals of the population, preferably from postcranial remains.

The Southern Chamois (*Rupicapra pyrenaica)*

The Southern chamois is a small-sized bovid, smaller and lighter than a mountain goat, which currently extends in the Cantabrian Mountain Range, the Pyrenees, and the Central Apennine Mountains (Herrero *et al*. 2020; Corlatti *et al*. 2021). Adult body mass is around 30 kg in males and 24 kg in females (Pérez-Barbería & Palacios 2009), and both sexes present two small, hooked horns. The chamois is a species that lives in alpine pastures and mountain forests, rocky areas, forested valleys, and lower slopes in mountainous regions (Herrero *et al.* 2020). In spring, it usually descends to feed during lactation and, in summer, it usually returns to higher altitudes to find shelter. It is a gregarious species, where the composition of the herds changes seasonally, responding to resource availability and reproductive cycles (Pérez-Barbería & Nores 1994). The sex-ratio is often biased towards females for Cantabrian populations and can fluctuate a lot due to under-exploitation of females in recreational hunting (González-Quirós *et al.* 2009; Serdio *et al.* 2009). Nevertheless, in non-hunted chamois populations within the Pyrenean National Park (French Pyrenees), no statistical difference was found between sexes after 8 years of survey (i.e. ratio males/female of 1/1.3; Gonzalez & Crampe 2001). From studies of survival by sex in Southern chamois populations in the French Pyrenees, Loison (2004) suggests that the sex ratio in the population is naturally biased in favour of females, even in non-hunted populations, because the survival rate of males declines more rapidly with age than that of females (Loison *et al.* 1999). However, under favourable environmental conditions, male survival is generally higher in low-density populations but of the same is not observed for females, so that the sex-ratio bias in favour of females is less pronounced (Toïgo & Gaillard 2003).

According to the current fertility parameters of the Southern chamois from Cantabrian Mountain Range (Pérez-Barbería *et al.* 1998), the juvenile phase covers the first three years of life (0–3 years) since ovulation occurs after three years (90.4% of females), and no female has been observed to ovulate at ages one and two. In the French Western Pyrenees (Bazès, France), however, for a population of *R. p. pyrenaica* the first breeding occurred at the age of 2 or 3 years, so that most females ≥4-years-old could be reasonably considered as multiparous (Kourkgy *et al.* 2016). However, it is worth noting that reproductive success can experience large annual variations in non-hunted populations, being density, climate, and body mass of females the most influential factors for ungulate species (Riney 1982; Bauer 1985; Loison 2004; Palacios 2009). The adult phase usually ranges from 3 to 10 years, and from 11 years onwards individuals enter a senescent phase, in which birth rates are reduced by 50% (Pérez-Barbería *et al.* 2010) and mortality rates increasing up to 90% (Crampe 1997). Nonetheless, the longevity of this species is very high, sometimes exceeding 20 years (e.g. Crampe 1992).

These fertility parameters are very similar to those shown by Alpine populations of *Rupicapra rupicapra* (Corlatti *et al.* 2021). Births are usually represented by a single kid, and twins are rare (Couturier 1938), with females breeding for the first time from three years of age (Schröder 1971), although this may be influenced by nutrition, climate, and density. Pregnancy probability is age-dependent and probably density-dependent, being 0% for females aged 0 to 2 years, 50% for 3 years, 90% for those aged 4 to 10 years and 83% for individuals older than 11 years (Valentinčič *et al.* 1974). These populations show fertility peaks between 4 and 7 years with reproductive senescence starting at 8 years (Morin *et al.* 2016), although other studies and populations support a reproductive senescence starting at 16 years (Tettamanti *et al.* 2015). A reproductive strategy seems to exist in older females in which pregnancies occur in alternate years, thus increasing reproductive success (Morin *et al.* 2016). Regarding to female survival senescence, it starts at around 7 years of age in the population of the Massif des Bauges in the French Alps, while in populations of the Swiss National Park it occurs at around 12 years of age (Bleu *et al.* 2015). This may be related to the hunting activity suffered by the former, which may affect their life-history strategies, as suggested Bleu *et al.* (2015). Maximum longevity records for *R. rupicapra* populations in the Swiss Alps National Park is 22 years old (Corlatti *et al*. 2012).

The origin and phylogenetic relationships of this species are difficult to establish due to the scarcity and dispersal of remains, defined these as a mystery by Professor Björn Kurtén (1968). Its classification has been subject to continuous revisions throughout the last century, defining up to three species, which has led to continuous changes in its classification (Pérez *et al.* 2013). For instance, due to its resemblance to goats, Linnaeus (1758) included the chamois in the *Capra rupicapra* species. Later, in 1816, Blainville created a new genus for this group, including it in the *Rupicapra rupicapra* species (see Domínguez Sanjurjo *et al.* 2009). In 1845, Charles Lucien Bonaparte separated the Southern chamois from this group, creating the species *R. pyrenaica*. In 1913, Lydekker grouped all the populations in *R. rupicapra* and, a year later, Camerano (1914) separated them into three: *R. pyrenaica* in the Iberian Peninsula, *R. ornata* in the Italian Apennines and *R. rupicapra* in the rest of Eurasia (see Domínguez Sanjurjo *et al.* 2009). A new revision carried out by Couturier (1938) included all them again in *R. rupicapra* but defining ten different subspecies. A new review, by Lovari (1987) and Nascetti *et al.* (1985) regrouped them into two species: *R. pyrenaica* in Southwestern Europe and *R. rupicapra* in the rest of Europe and the Caucasus; and, in turn, divided them into ten subspecies, each one distributed in a different mountain range (Domínguez Sanjurjo *et al.* 2009). One of the latest reviews combining genetic, morphological and distribution studies points again to the existence of seven species (Groves & Grubb 2011). This classification includes *R. parva*, *R. pyrenaica*, *R. ornata*, *R. rupicapra* (including the chamois of the Alps, Tatra, and Chartreuse Mountain ranges), *R. carpatica*, *R. balcanica* and *R. asiatica* (including the populations of Turkey and the Caucasus). Other authors, following this scheme, include the Balkan chamois in *R. rupicapra* (Valdez 2011).

Phylogenetic analyses based on studies of mtDNA, microsatellite sequences and the Y chromosome provide data that differ greatly from the analyses performed by Groves & Grubb (2011) and Valdez (2011), reclassifying chamois back into a maximum of three species (Pérez *et al.* 2013). Moreover, according to mtDNA three clades are distinguished: one for the Western European populations (*R. p. parva* and *R. p. pyrenaica* and small alpines population of *R. r. rupicapra*), another for the Central European groups (*R. p. ornata* and *R. r. cartusiana*) and the last for the Eastern European populations (the other six populations) (Pérez *et al.* 2013). On the other hand, microsatellite analysis separates three groups: *R. pyrenaica*, *R. rupicapra* and *R. ornata*. Finally, according to the Y chromosome analysis the populations can be divided into the two known species: *R. pyrenaica* and *R. rupicapra* (Pérez et *al.* 2013). In the present work, we consider that populations of Iberian chamois are included in the *Rupicapra pyrenaica* species.

So far, the oldest presence of the Southern chamois in Western Europe is associated with *Rupicapra* cf. *pyrenaica* in a 440,000-year-old level in Arago (Rivals 2002, 2004). However, the appearance of the genus *Rupicapra* sp. was clearly identified in South-eastern Europe at the Early and Middle Pleistocene transition at Kozarnika (Bulgaria) in levels associated with Brunhes palaeomagnetic instability (780–750 ka) (Fernandez & Crégut-Bonnoure 2007). In addition, the genus could be present among the remains of a rupicaprini from the Early Pleistocene at the site of Trlica in Montenegro (Crégut-Bonnoure & Dimitrijevic 2006; Crégut-Bonnoure 2007). A filiation between the genus *Rupicapra* with the ancestral form *Procamptoceras brivatense* has been suggested by Fernandez & Crégut-Bonnoure (2007). This is in line with the divergence between the three main mtDNA clades of *Rupicapra* that has been estimated at the Early Pleistocene around 1.9 Ma (Pérez *et al.* 2014, 2017a).

It has been suggested that *R. pyrenaica* spread from Asia to the Iberian and Italian peninsulas during the Middle Pleistocene (Crégut-Bonnoure 2006), and during the Late Pleistocene, this species was distributed throughout the Iberian Peninsula, thus suggesting great adaptive versatility (Cardoso & Antunes, 1989; Riquelme Cantal 2008; Arsuaga *et al.* 2010). During the final Late Pleistocene, between 43,000 and 10,000 years, the divergence could have occurred between the two species of the Iberian Peninsula, on the one hand, and the species occupying the Caucasus, the East of Europe, and the Alps, on the other hand. Finally, during the late Holocene the differentiation between neighbour populations would have occurred (see details in Pérez *et al.* 2017b).

The Cave of Valdegoba

The Cave of Valdegoba (42°32′36″N 3°46′27″ W) is located 28 km distant from the city of Burgos (N Spain), 930 m above sea level and 35 m above the current course of the Urbel River (Fig. 1). The cave is in the southernmost foothills of the Cantabrian Mountain Range, located in a large Turonian limestone outcrop (Late Cretaceous), which has been cut by the Urbel River, creating a small canyon that provides access to the tertiary Duero basin (Quam *et al.* 2001). Between 1987 and 2006, five excavation campaigns were carried out in this site, providing huge faunal and lithic assemblages. Among these, 15 human remains from five different individuals stand out, including a specimen with traits like those of Neanderthals (Quam *et al.* 2001; Arceredillo 2016).

During these excavation campaigns, several test pit excavations were also carried out at the site. However,

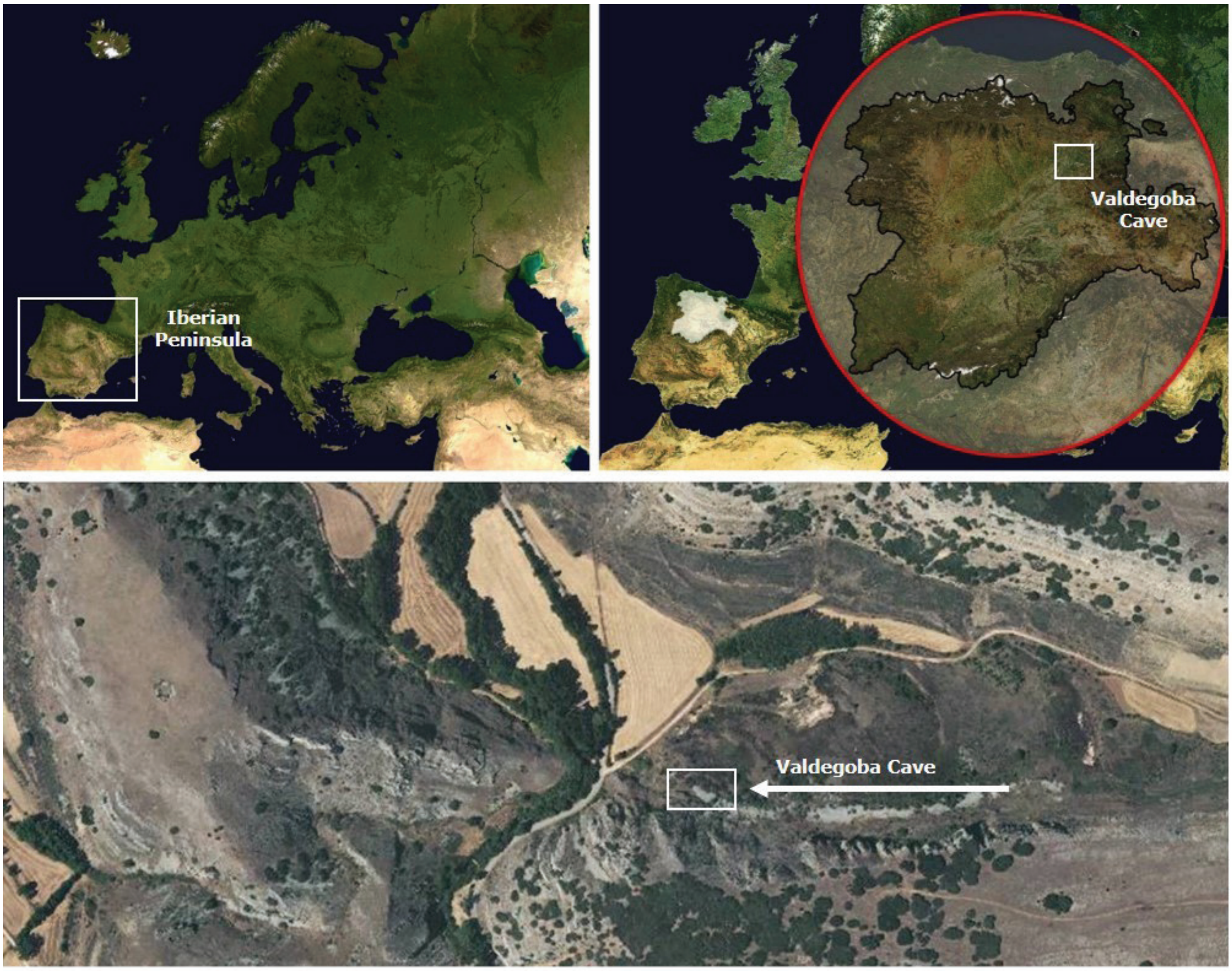

Fig. 1. Geographical location of Valdegoba site.

due to stealing from fossil poachers and karst reactivations, materials were found only at one of them. These test pit excavations allowed to describe Valdegoba's stratigraphy, which consists of eight levels often difficult to distinguish (see Díez *et al.* 1989) that are classified in six stratigraphical units (A-F), from bottom to top, as follows:

A. (Level I): Basal stalagmitic flowstone. Sterile.
B. (Level II): Red clays with silts and sands and a sub-level of carbonated concretions. Sterile.
C. (Level III): Brown clays with silts and sands. Stalagmitic concretions on the surface. Sterile.
D. (Levels IV-VI): The level IV presents brown clayish sands with calcareous rocks not exceeding 50 cm thick. Visible erosion on the surface. Lithic industry and faunal remains. The bottom of the unit has a breccia covered by limestone blocks, lithic tools and fossils.
E. (Level VII): A laminar stalagmitic concretion closes unit D. This concretion is attached at various points to the walls and ceiling. It presents archaeological material. It is a clear indication of the clogging the cavity reached.
F. (Level VIII): Clays in contact with unit E. It contains a mixture of Palaeolithic and Holocene materials, as well as human remains. This mixture is a clear indication of disturbance caused by despoilers.

Different analyses of some of these levels have provided age estimates for this site. The U/Th dating analyses conducted by James Bischoff (US Geological Survey, Menlo Park, California) provided inconclusive results. Three samples were analysed, one from the basal flowstone from Level I, and two from the capping speleothem from Level VII. The first of these samples provided a date greater than 350 ka. The other two gave values of 95 ± 8 ka and 73 ± 5 ka, respectively. However, these samples were contaminated with detrital thorium, thus implying an overestimation of their dating. Therefore, it was concluded that the layer of speleothems from Level VII must have had an age of less than 73 ka (see Quam *et al.* 2001). More recent dating with ^{14}C at level V provided average values of 48.5 ka (Dalén *et al.* 2012).

Thousands of remains of lithic tools (2,147 lithic pieces) and fauna have been recovered from the excavation works at Valdegoba site. The obtention of environmental resources by these hominins was carried out with an industry of different raw materials, including flint, quartzite, sandstone and autochthonous quartz recovered from a short distance to the cavity, although most tools were developed on quartzite and flint (Quam *et al.* 2001; Terradillos-Bernal & Díez Fernández-Lomana 2018). The discoid and Levallois techniques were the most common in the site, but spheroids are qualitatively relevant with the production of laminar supports. Scrapers are the most abundant tools, but points and compound tools are also well represented (Quam *et al.* 2001, Terradillos-Bernal & Díez Fernández-Lomana 2018). This industry can be included within the variability described in other sites of the Middle Palaeolithic (Moure Romanillo *et al.* 1997). Faunal remains cover a diverse range that includes species of different orders of mammals: Artiodactyls (*Bison priscus, Bos primigenius, Capra pyrenaica, Capreolus capreolus, Cervus elaphus, Rupicapra pyrenaica, Sus scrofa*), Perissodactyls (*Equus ferus, Equus hydruntinus, Stephanorhinus hemitoechus*), Carnivores (*Canis lupus, Vulpes vulpes, Felis silvestris, Lynx pardinus, Panthera pardus, Crocuta crocuta, Lutra lutra, Martes* sp., *Meles meles, Ursus arctos, Ursus spelaeus*), Primates (*Homo sapiens, Homo neanderthalensis*), Eulipotyphla (*Neomys* sp., *Sorex* sp.), Rodentia (*Apodemus* cf. *sylvaticus, Arvicola* sp., *Castor fiber, Hystrix* cf. *vinogradovi, Marmota* cf. *marmota, Microtus nivalis, Microtus arvalis-agrestis, Pliomys lenki*) and Lagomorpha (*Oryctolagus cuniculus*) (Díez *et al*., 1989). In addition to these mammals, the Valdegoba faunal assemblage includes bird species such as *Aegypius monachus, Alectoris* sp., *Anas* sp., *Athene noctua, Columba* sp., *Coturnix coturnix, Falco tinnunculus, Pyrrhocorax graculus,* and *Turdus* sp. (Díez *et al.* 1989; Arceredillo 2016).

Taphonomic analyses carried out on the remains of herbivores suggest that Neanderthals had primary access to the carcasses (Díez 2006), and the study of seasonality in ungulates indicates that the occupation of the cave happened throughout the year, with an alternation between carnivores and hominins (Arceredillo 2015), although the percentages of accumulation made by both agents is unknown (Díez 2006). Furthermore, there is also evidence of the consumption of carnivores by hominids (Díez 2006). Herbivores make up most of the recovered record, representing 87% of the faunal assemblage, and the chamois (*R. pyrenaica*) is the most abundant species, almost 60% of the remains (Quam *et al.* 2001). This collection of Southern chamois, with more than 4,000 remains, is the second most abundant in the Iberian Peninsula after the Amalda site (Gipuzkoa) (see Altuna 1990), and is also the best preserved (Díez Fernández-Lomana *et al.* 2014). The remains of the chamois were initially classified as belonging to the species *R. rupicapra* (Quam *et al.* 2001; Navazo *et al.* 2005; Díez *et al.* 2008) although according to Crégut-Bonnoure (2006) this species was never able to cross the Pyrenees. New phylogenetic and migratory studies have greatly influenced the classification of the Southern chamois, classifying in some cases as *R. rupicapra* and in others as *R. pyrenaica*, as discussed above.

Mortality profiles, life tables, and weight estimates

Sex, age at death and body mass are fundamental sources of information to characterize a species at an ethological and biological level, and they are also essential parameters to study the population dynamics of Southern chamois from Cantabrian Mountain Range (Pérez-Barbería & Pérez-Fernández 2009). Also, these variables can provide relevant data on the hunting and subsistence strategies of populations in the past (Stiner 1990), allowing us to understand the composition of a group and the possible origin of accumulations (Klein & Cruz-Uribe, 1984; Monchot 1999). However, neontological observational methods cannot be applied directly in archaeology because the source of information is not actually the living organisms, but their fossil remains, having to infer the biological characteristics of the fossil species indirectly. Furthermore, the sites usually present an additional difficulty due to the fragmented nature of many remains and the absence of diagnostic material, making the determination of these variables complex (Arceredillo 2015). For these reasons, in this study, analytical tools have been developed and applied to increase the information on fossil populations. These include both life tables and ternary diagrams to study mortality patterns as well as the use of allometric equations to estimate the mass of the individuals that were part of the population.

Mortality profiles represent an important source of palaeoecological information, allowing us to understand the origin of an accumulation or the causes of animal death. These profiles show great variability among the archaeological sites (Lyman 1994; Steele 2002, 2004; Fernandez 2009) and it is sometimes impossible to infer the accumulating agent (Twiss

2008). Nevertheless, it is possible to identify if the accumulation represents a random sample of the individuals from the original population or, on the contrary, if any accumulating agent biased the record (e.g. Arribas & Palmqvist 1998; Palmqvist & Arribas 2001; Blasco *et al.* 2011; Saladié *et al.* 2018). In palaeontology and zooarchaeology, two theoretical models were proposed to define the type of mortality profile: the diachronic or attritional model, which assumes that the individuals of the fossil sample were accumulated at different times; and the catastrophic or synchronous one, which makes the strong assumption that all or most of the individuals died at the same time due to some natural disaster or to hunting strategies that similarly impact all age classes of the population (Shipman 1975; Haynes 1987, 1988; Kahlke & Gaudzinski 2005; Lyman 1987, 1989). In the diachronic model, the distribution of individuals mostly shows an overrepresentation of young and senile specimens compared to prime-age adults, due to their lower survival rates in hostile conditions (e.g. deaths from predation, epizooty, etc.), as they are the most vulnerable age classes (Klein 1982a, 1982b; Stiner 1990). For this reason, this model is often referred to as U-shaped. In the catastrophic or synchronous model, the distribution of fossil individuals decreases in abundance from the youngest to the most senescent age classes, reflecting the living structure of the population since all or most of the individuals are present in the fossil assemblage. This model is often referred to as L-shaped and is associated with catastrophic death events (Stiner 1990, 1991; Menéndez *et al.* 2016). Both models are related to each other since the catastrophic profile reflects the composition in life of the whole population, while the diachronic or attritional one refers to the deaths that took place within its age classes.

One way to analyse and compare mortality patterns is to use the ternary diagrams first defined by Greenfield (1986, 1988) for the Neolithic period and used afterwards by Stiner (1990) for the Pleistocene. In these diagrams the mortality profiles of the species are located in the graph according to their percentage of individuals calculated from three major age groups from different lifespan phases: the juvenile, the prime adult and the old adults including senescent phases. Stiner (1990) defined different areas to classify mortality with a special emphasis on U- and L-shaped profiles related to attritional and catastrophic patterns, respectively. In later works, the limits of these areas have been reassessed, first by bootstrap resampling (Steele & Weaver, 2002) and then by a likelihood approach that better takes into account when any of the age classes have counts of zero (Weaver *et al.* 2011). Similar findings have been made by Discamps & Costamagno (2015) who recently provided new areas that take into account the duration of the three phases (juveniles, prime adults and old adults) according to each species.

Both mortality profiles and ternary diagrams have been used to analyse the exploitation of animal resources by Middle Palaeolithic human populations (e.g., Gaudzinski 1995; Gaudzinski & Roebroeks 2000; Hoffecker & Cleghorn 2000; Valensi & Psathi 2004; Alder *et al.* 2006; Yeshurun *et al.* 2007; Rendu 2010; Domínguez-Rodrigo *et al.* 2015; Rodríguez-Hidalgo *et al.* 2017; Marín *et al.* 2017). From these studies, it was possible to infer that Neanderthal hunting strategies focused predominantly on prime adult individuals (Gaudzinski & Roebroeks 2000; Hoffecker & Cleghorn 2000; Valensi & Psathi 2004; Alder *et al.* 2006; Yeshurun *et al.* 2007; Domínguez-Rodrigo *et al.* 2015; Rodríguez-Hidalgo *et al.* 2017); but in other cases had broader profiles (Marín *et al.* 2017); in some sites no evolution in these strategies was observed over time (Valensi & Psathi 2004) whereas in others it was observed (Rendu 2010). It was also possible to infer that Neanderthals adapted their hunting and consumption behaviours to the environmental conditions (Gaudzinski 1995; Hoffecker & Cleghorn 2000; Yeshurun *et al.* 2007; Rendu 2010), and that these populations exhibited subsistence behaviours no different than those of current hunter-gatherer populations (Hoffecker & Cleghorn 2000; Alder *et al.* 2006; Yeshurun *et al.* 2007), among other aspects. This is a sample of the possibilities of the use of these tools in the study of Neanderthal resource exploitation.

In addition to ternary diagrams, standard methods in population ecology allow the analysis and reconstruction of the mortality patterns of species in different palaeobiological contexts. One of them are life tables, which were initially used in laboratory conditions to understand the lifespan, survival and mortality patterns of insects (e.g. Pearls & Miner 1935). Whereas the traditional life tables were applied in life sciences from living individuals (see Deevey 1947), in palaeobiology the set of dead individuals in each age interval represents the main source of information of the different cohorts of a population (Kurtén 1953a, 1953b, 1954, 1983; Van Valen 1963, 1964, 1965; Voorhies 1969; Koike & Ohtaishi 1987; Fernandez & Legendre 2003; Mihlbachler 2003; Fernandez *et al.* 2006; Fernandez & Boulbes 2010; Monchot *et al.* 2012; Price *et al.* 2016; Fernandez *et al.* 2017; Pérez-Pérez *et al.* 2021). In palaeobiological context, life tables are used from a long-term perspective, using individuals of all ages that could belong to different cohorts considering that the fossil record is a random representation of the individuals in a population reflecting its structure. Life tables allow inferring autecological parameters including, among others, survival and mortality rates, mean generation time of the population, and to estimate whether the population is growing, declining or stable. In addition, it is possible to make comparisons of demographic parameters between different populations of the same species or at interspecific levels, or even between different zoological groups.

As an extension of the life tables, other mathematical tools, such as Leslie-Lewis matrices or the Weibull model, have also been used in different palaeobiological contexts to make projections of key demographic parameters (Fernandez & Boulbes 2010; Monchot *et al.* 2012; Rodríguez-Gómez *et al.* 2013, 2014a, 2016a, 2016b, 2017a, 2017b, 2017c, 2020, 2022; Martín-González *et al.* 2016, 2019; Domingo *et al.* 2017; Fernandez *et al.* 2017).

As discussed above, body mass is another important parameter when the nature and dynamics of a population is analysed. Inferring the mass of large mammals from their fossil remains, both cranial and postcranial, is a relevant field of study in palaeontology (see Damuth & MacFadden 1990). Normally, these methods consist of using allometric equations derived from modern species that relate the skeletal dimensions of the individuals with their body mass (e.g. Scott 1990; Van Valkenburgh 1990). In this way, if the site has enough fossil material and its state of preservation is relatively good, the average mass of the population can be estimated. This can be useful to compare it with other populations from different regions or chronologies, analysing the differences and trying to infer the factors involved in them.

Material and methods

Valdegoba site has provided an important collection of chamois remains. This species is represented mainly in the unit D (Arceredillo *et al.* 2011), with a total of 4,482 identified remains, of which 3,857 were craniodental elements and 1,177 postcranial ones. All the remains used in this study come from this unit.

In the cavity, a minimum number of individuals (MNI) total of 114 were identified, 26 immatures (kids, yearlings and other subadults) and 88 adults, according to the dental material (Arceredillo 2015). The remains of this species are more abundant at unit D when occupation by the Neanderthals was more intense. At the top of unit D, close to unit E, there is significantly lower human presence that has been interpreted as a change in the hunting preferences for the other species that occupied the cavity at that time (Arceredillo *et al.* 2011). Adult chamois fossil remains are more abundant, and their accumulation seems to have occurred throughout the whole year. The analysis of sexual dimorphism carried out using the K-means method, revealed that the males were larger than the current ones and that the females showed a similar size (Arceredillo *et al.* 2011). This implies a greater sexual bimodality than in the current Southern chamois (Arceredillo *et al.* 2011; Arceredillo 2016). An isotopic analysis conducted from chamois remains has revealed that they had a wide range of $\delta^{13}C$ values, which indicates a diverse diet (Feranec *et al.* 2010).

Taxonomic assignment of the remains was carried out using osteological atlases (Barone 1966; Pales & García 1981). As described previously, thousands of pieces, both cranial and postcranial, were recorded for chamois in the Cave of Valdegoba. For the study of the population profile, we used the age estimates starting from the teeth and, for calculating the body masses, we used postcranial remains since dental material offer less precise values (e.g. Damuth 1990; Fortelius 1990).

In the reconstruction of the population profile of the chamois, we used the age at death of the individuals as estimated by Arceredillo (2015) from the equations of Klein & Cruz-Uribe (1984). These estimates were made from the most frequent dental rank, D_4 in the case of immature individuals, and M_1 for adults. To avoid considering the same individual twice from the age calculations based on the two teeth for establishing the MNI, the estimates of D_4 for individuals above 12 months of age and those of M_1 for individuals below 12 months were both excluded. Thus, we only considered the D_4 corresponding to the first year of life and the M_1 for older animals. To avoid considering the same individual several times, we only selected the D_4 and M_1 from the left hemimandibles because the conservation was better although the latter were less abundant than the right ones (155 right specimens, versus 122 left). According to this ratio the differential preservation is good with 78.7% (100% would have been 155 right vs 155 left specimens). In this way, the total number of individuals available to reconstruct the mortality profile of Valdegoba's chamois was 112, reaching a maximum longevity of 18 years, according to Arceredillo (2015). We defined the age intervals up to the maximum longevity in one-year intervals and distributed the 112 individuals according to the calculated age.

For the life tables analysis, we used the time-specific or static model that is suitable for multiple fossil deposits through time. Theoretically, only demographic parameters of females are considered in life tables (Gaillard *et al.* 2003). This is simply because paternity of large mammals is usually unknown, so numbers of offspring per male cannot be estimated. However, it is widely accepted that male survival does not affect the population growth rate of most natural mammalian populations (Caswell & Weeks, 1986), as it is observed in Alpine chamois with non-biased survival by sex (Corlatti *et al.* 2012). Consequently, considering realistic balanced sex-ratio at birth (e.g. 1:1 in this study), the fecundity rates for each age interval must be divided by a factor 2 in order to count all the individuals of the life table (Gaillard *et al.* 1998; Monchot *et al.* 2012; Fernandez *et al.* 2017).

We assume here a stationary age structure through time with constant survival and fecundity rates for the different cohorts even if they are not required for the time-specific model (e.g. Sinclair 1974; Ricklef & Miller 1999). We also assume that the age structure of the different cohorts corresponds to a local population and that migration flows are random and did not modify the sample (Caughley 1977; Caughley *et al.* 1994). We should keep in mind that in current ecological studies these strict assumptions are unlikely to be met in any population of wild mammals because opportunities to monitor entire cohorts for long periods of time are unlikely (Menkens & Boyce 1993; McCullough *et al.* 1994; Gaillard *et al.* 1998).

These tables are built using different demographic parameters (see Fernandez *et al.* 2017), where: 'x' is the age interval, which is one year in the present analysis. In zooarchaeological studies, there is often confusion or a lack of agreement in the definition of the terms 'age interval' and 'age class' (in months, year or any time interval). Strictly speaking the former begins at 0 and the latter at 1 (Caswell 2001). In this study, we follow this author in adopting the term 'age interval'. For example, any value in the first interval x_0 will refer to the first year of life beginning to 0 and ending at 1 years (12 months). The interval x_1 will refers to the second year of life beginning at 1 year and ending at 2 years old, and so on. 'd_x' is the proportion of individuals dying between ages $_x$ and $_{x+1}$: $d_x = l_x - l_{x+1}$; 'l_x' is the proportion of individuals in the cohort that survive in an age class: $l_{x+1} = (l_x - d_x)$, usually the initial value can be set to 1 (as in this study), 100 or 1000 in the first age interval; 'q_x' is the mortality rate from one interval to the following: $q_x = d_x / l_x$; 's_x' refers to the age-specific survival rate from one age class to the next: $s_x = l_{x+1} / l_x$; 'm_x' corresponds to the number of offspring per female in each interval. Fertility values for each age interval in Valdegoba's chamois are unknown. For this reason, we used data reported for various current populations (Crampe *et al.* 2004; Jones *et al.* 2009; Pérez-Barbería *et al.* 2010). Given the similarities between fertility parameters between Southern and Alps chamois (see above), we applied the same (m_x) values for all the current populations except for the New Zealand chamois, which were given by Caughley (1970); 'R_0', the net reproductive rate corresponds to the average number of offspring produced by an individual during its lifetime. It is therefore considered as the average reproductive success of the population with the following calculation: $R_0 = \Sigma\, l_x m_x$. Thus, when R_0 is <1, the population decreases while it is increasing when R_0 is >1, being stable when it equals 1. We also used the mean generation time 'T' which provides the average interval between the birth of an individual and the birth of its offspring. The age of the individuals (x) is multiplied by the proportion of individuals surviving to that age (l_x) and the average number of offspring at that age (m_x). This calculation is performed for each age interval, and the values are added together and divided by (R_0) such as: $T = \Sigma\, l_x m_x / R_0$.

The time-specific life table model provides a picture of a population according to its demographic parameters. Simultaneously, the projection in time of the entire population is one of the best ways to characterize the initial state of a population and therefore its viability through time. In order to make projections of the population size of *R. pyrenaica* from Valdegoba and current species of *Rupicapra*, we used the simple pre-breeding Leslie-Lewis model (e.g. Lewis 1942; Leslie 1945, 1948; Caswell 2001) with the software PopTools (Version 3.2.3.) developed by Hood (2010). Here, we will not delve into different matrix formulations as a step-by-step procedure has already been described at length with case studies for different species in various palaeobiological contexts with this model (Fernandez *et al.* 2017). As an example, the following matrix (A) of 13 age intervals will depend on the life table fecundity m_x distributed in the first row (m_0, m_1, m_2, etc.) as well as the age-specific survival rate (S_0, S_1, S_2, etc.) in the sub-diagonal, both to be multiplied by the state vector $n(t)$ such as: $An(t) = n(t+1)$

$$\underset{A}{\begin{pmatrix} m_0 & m_1 & m_2 & \cdots & m_{12} \\ S_0 & 0 & 0 & \cdots & 0 \\ 0 & S_1 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & 0 \\ 0 & 0 & 0 & S_{11} & 0 \end{pmatrix}} * \underset{n(t)}{\begin{pmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \\ \vdots \\ n_{12}(t) \end{pmatrix}} = \underset{n(t+1)}{\begin{pmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \\ \vdots \\ n_{12}(t+1) \end{pmatrix}}$$

The state vector values $n_0\,(t)$, $n_1\,(t)$, $n_2\,(t)$ are simply the fraction of the total number of individuals (l_x) from the life table in each age interval. The product of $An(t)$ gives the projection of the matrix $n(t+1)$, which is the new number of individuals at the next succeeding census of the projection interval. Thus, it is possible to calculate the lambda (λ) which is a crucial ratio of the population size in one year relative to that in the preceding year, such as $n(t + 1) = n(t) * (lambda)$ (see also Caswell 2019, eq. 9.13). Once the stable age distribution has been reached, the lambda, also known as the asymptotic growth rate, has the remarkable property to remain stable and to correspond to the dominant eigenvalue of the Leslie-Lewis matrix model. Consequently, the population size will maintain ($\lambda = 1$), grow ($\lambda > 1$) or shrink ($\lambda < 1$). To have a complete picture, we also gave the damping ratio (ρ) from the population projection matrix which estimates the transient dynamics that is the time taken by a population to converge to a stable age structure following a perturbation. (ρ) is determined by the ratio of the dominant eigenvalue to the second largest eigenvalue: $\rho = \lambda 1 / |\lambda 2|$ (see Caswell 2001, p. 95). The larger the ρ, the quicker the population converges to age stable distribution (Menkens & Boyce 1993). The calculation was made using the software R (version 4.1.0) and the package 'popbio' (Stubben & Milligan 2007).

The age structure of the chamois from Valdegoba allows to estimate the mortality pattern using the ternary diagrams defined by Greenfield (1986) and modified later by Stiner (1990) and more recently by Discamps & Costamagno (2015). Age intervals of one year previously described were associated to different phases of lifespan: juveniles, 0–3 years or 0–36 months; prime adults, 4–10 years or 36–120 months; and, old adults, 11–18 years or 120–216 months.

In addition to life tables, the mean body mass of the chamois from Valdegoba was estimated to determine its physical characteristics. Mass estimates were derived from postcranial elements (humeri, radii, metacarpals and metatarsals (see Table 1), and allometric equations for bovids were applied according to the work of Scott (1990; in Damuth & MacFadden 1990, table 16.7) (Table 1). Several specimens were used for each measurement: in the case of humeri, 13 specimens were selected for measurements Hm4 and Hm5; 24 for radii (23 with values for Rd2 and 24 for Rd4); 27 for metacarpals and 20 for metatarsals (see Table 1). When two measurements of the same specimen were available for different variables, the mass value was averaged between the estimates. A total of six variables have been measured from 84 bones (see Table S1) using a digital calliper up to the tenth of a millimetre, according to Driesch (1976). The selected bones belonged only to adult specimens (with fused epiphyses), given that the equations are developed for them.

Table 1. Values of the equations used to calculate body mass of *Rupicapra pyrenaica* from Valdegoba site. These equations were derived from single limb bones in bovids by Scott (1990). Hm4: transversal diameter of distal articular surface in anterior view of the humerus; Hm5: maximum transversal diameter of distal epiphysis of the humerus; Rd2: transversal diameter of proximal articular surface of the radius; Rd4: maximum transversal diameter of proximal epiphysis of the radius; Mc2: transversal diameter of proximal articular surface of the metacarpus; Mt4: maximum transversal diameter of distal epiphysis of the metatarsus. The equation has this form: $\log (BM) = b (\log X) + c$, where BM is the body mass in kg and X is the measure of bones (in cm) in each case.

Bones	**Variables**	**Slope (b)**	**Intercept (c)**	**r²**
Humerus	Hm4	2.550	0.408	0.9590
Humerus	Hm5	2.625	0.276	0.9604
Radius	Rd2	2.507	0.431	0.9629
Radius	Rd4	2.431	0.374	0.9543
Metacarpus	Mc2	2.650	0.602	0.9529
Metatarsus	Mt4	2.650	0.602	0.9529

In order to calculate the average mass of the population, the proposal of Rodríguez-Gómez *et al.* (2022) was followed:

$$B = \sum (R_i * M_i * D),$$

where B is the biomass of the population, R_i the proportion of individuals of the population in class i, M_i the average body mass of the individuals of class i, and D the population density, which in this analysis equals 1 since the aim is to know the average mass of the population. Therefore, the proportion of individuals in each age class (R_i) and their average mass (M_i) must be estimated. To calculate the relative proportion of each age class (R_i), we used:

$$R_i = \frac{l_i}{\Sigma l_i},$$

where l_i is the proportion of individuals in class i. The values of l_i used to estimate R_i were obtained from the life table established for the chamois population of Valdegoba.

In order to estimate the mass of all age intervals, from birth to adult size, the approximation of Zullinger *et al.* (1984) was used:

$$M(t) = A * e^{-e^{-K(t-I)}},$$

where A is the asymptotic mass (i.e., the adult body mass, ABM), $M(t)$ is the mass (g) at age t, K is the growth rate constant (days^{-1}), and I is the age at the inflection point (191.2 days). K relates to the mass of adults by the equation:

$$\log (K) = -0.901 - 0.302 * \log (M)$$

The average mass for each age class was estimated as the mean of extreme values into each age range.

In order to better understand the biological and demographics parameters of *R. pyrenaica* from Valdegoba, we compared our fossil cohorts (112 individuals) with current populations. We used the data from Loison *et al.* (1994), which focused on survival rates of the female chamois *R. rupicapra* (French Alps), including *R. pyrenaica* (French Pyrenees) (Crampe 1992) as well as *R. rupicapra* from New Zealand (Caughley 1970). It is worth comment that the demographic parameters in these studies were obtained using non-selective and random sampling methods, by collecting information from dead (Crampe 1992), marked (Loison *et al.* 1994) or hunted individuals (Caughley 1970). In addition to these analyses, we wanted to analyse how the conditions of stationarity and stability could affect the populations of *Rupicapra* in terms of the representation of their mortality patterns in ternary diagrams defined by Stiner (1990) and Discamps & Costamagno (2015). For addressing this, we reconstructed a hypothetical *Rupicapra* population with stable and stationary conditions and its mortality profiles from the Weibull model, following the procedure of Martín-González *et al.* (2016, 2019), who used the Weibull model to describe stable and stationary population structures for past species because this model has a good fitting for fossil populations. Weibull model is a parametric model used in survival rate analysis (Hosmer and Lemeshow, 1999), being a particular case within exponential type models (see Martín-González *et al.* 2016). Species' fertility values by age class are the entries used by the model to reconstruct survival and mortality profiles. We defined *Rupicapra* using the fertility values of the current species, considering a longevity of 18 years as proposed by Arceredillo (2015) for Valdegoba chamois. This approach provides a large number of outputs, for this reason, we selected the extreme living and mortality structures, with maximum and minimum subadult mortality (${}_{M}M$ and ${}_{m}M$, respectively), as well as their corresponding living structures with minimum and maximum subadult survival (${}_{m}S$ and ${}_{M}S$, respectively) (see Martín-*González et al.* 2016, 2019).

Results

Our results concerning the proportion of individuals (d_x) in each age interval, show that specimens from Valdegoba are distributed in 18 age intervals (Fig. 2). The

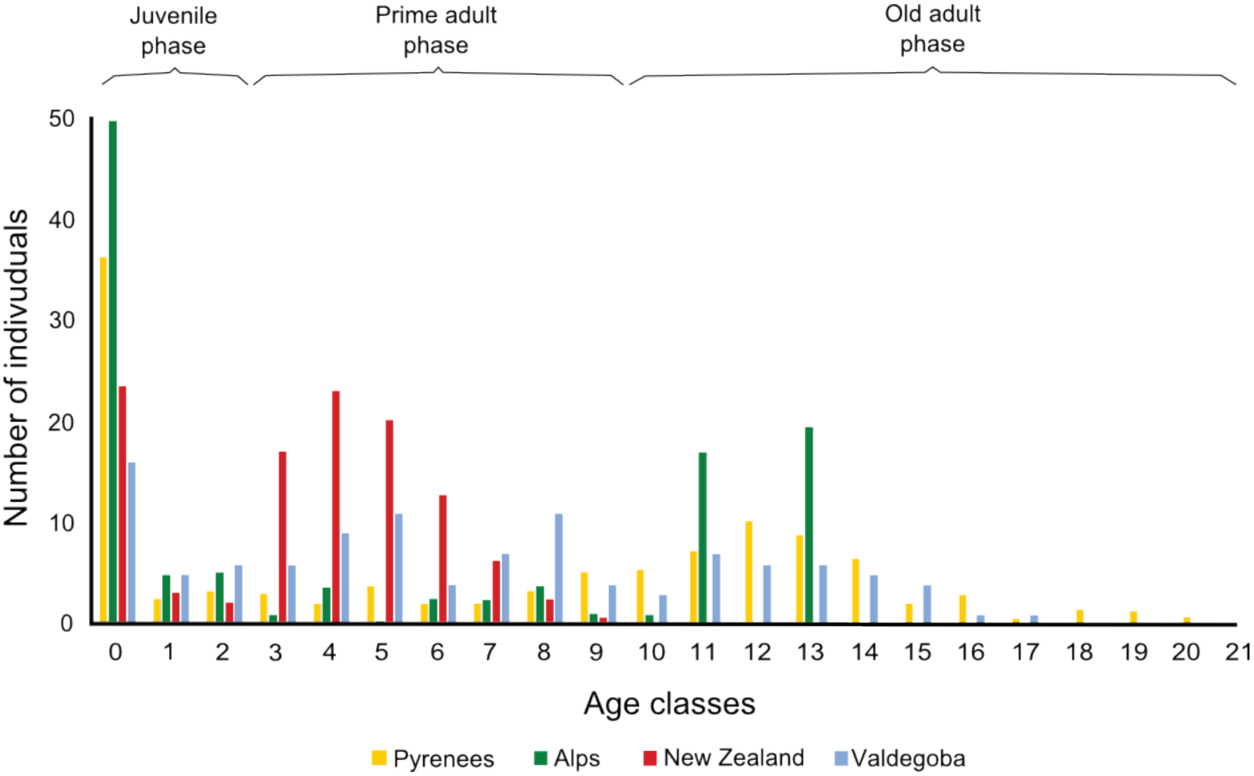

Fig. 2. Mortality profiles of *Rupicapra* populations compared in the present study, showing the number of dead individuals by age interval. In the case of Valdegoba, we obtained number of individuals by age interval from dental remains (see Arceredillo, 2015). In order to compare among mortality profiles, we reconstructed the profiles of recent *Rupicapra* populations (Caughley 1970; Crampe 1992; Loison *et al.* 1994) with the same total number of individuals as Valdegoba population (112 individuals).

population does not clearly indicate either a U-shaped or an L-shaped mortality pattern, as classically defined (see Introduction). The highest number of individuals is in the first year of life (n = 15), and the lowest numbers are distributed into the two last age intervals (n = 1, each) (Fig. 2). However, if Figure 2 is analysed without the first age class, the pattern would be similar to a bell-shape profile with a high plateau between classes 5 and 8, which correspond to the age intervals with the highest reproduction rate in current populations (Valentinčič *et al.* 1974; Pérez-Barbería *et al.* 2010; Morin *et al.* 2016). Within the penultimate adult phase of the lifespan, there is a progressive reduction of the frequency from the age interval 8 until the last age interval, representing senescent adults. The proportion of individuals increases from age interval 1 (n = 5) to reach 11 individuals in age interval 5 and 8 with a smaller proportion in age intervals 6, 7, 9, and 10 (Fig. 2). The Spanish population shows that the adult phase presents the highest number of individuals (46%), followed by the senescents (30%) and the juveniles (24%) (Fig. 2). To evaluate the general death pattern of Valdegoba, we plotted the percentages of individuals from each age phase both into the original ternary diagram of Stiner (1990) and into the one with revised zoning by Discamps & Costamagno (2015) (Fig. 3). The age structure of Valdegoba corresponds to a catastrophic profile or of living structure as defined by Stiner with a L-shaped curve (Fig. 3A) and to the U- or L-shaped profile corresponding to Juvenile Prime Old (JPO) zoning according to Discamps & Costamagno (Fig. 3B).

Given that the mortality pattern of Valdegoba chamois seems to correspond to a living population, we used the proportion of dead individuals in each age interval (d_x) as the starting point to build the life table of the Spanish fossil *R. pyrenaica* to be compared to the current populations of *Rupicapra* (Tables 2, S2). Our first result on the net reproductive rate (R_0) shows a value >1 (R_0 = 1.57) indicating growing population in Valdegoba (Table 2). This is the case for the closest current French Pyrenean population *R. pyrenaica* (R_0 = 1.69) as well as for the French Alps *R. rupicapra* with R_0 = 1.29; the New Zealand *R. rupicapra* population showing a perfect equilibrium with R_0 = 1.00 (Table S2). According to mortality and survival rates, the life table of Valdegoba shows an average mortality rate (q_x) of 0.26 and a survival rate (s_x) of 0.74 (Table 2), being age interval x_1 with the highest survival rate and x_{15} the highest mortality rate, in addition to the last one (x_{17}) where no individual survives to the next. The average fertility rate (m_x) for all age intervals of Valdegoba's population was 0.19, with a maximum (0.40) for intervals from 4 to 10 (Table 2).

According to the survival and fecundity rates obtained from the life table of Valdegoba chamois, a

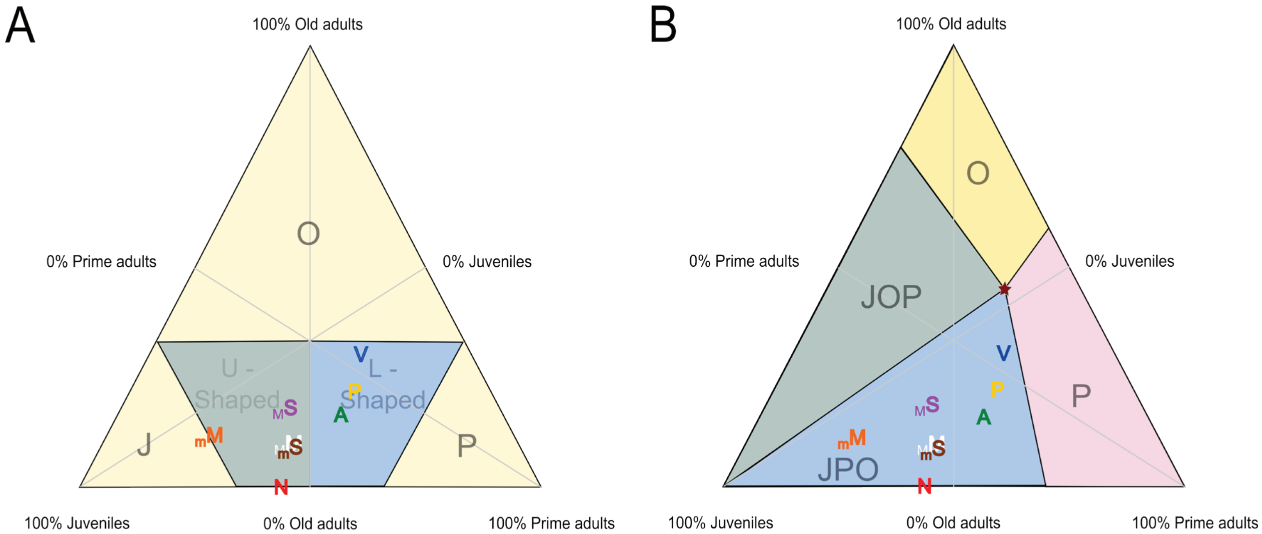

Fig. 3. Ternary diagrams representing modern populations of *Rupicapra pyrenaica* from the Pyrenees (P) (Crampe 1992) (29% juveniles (j); 49% prime adults (a); 22% old adults (o)) and the Alps (A) (Loison *et al.* 1994) (35% j; 48% a; 17% o) and *Rupicapra rupicapra* from New Zealand (N) (Caughley 1970) (56% j; 44% a; 0% o) compared with the population profile of Valdegoba (V). In addition, mortality ($_{\mathrm{m}}$M: minimum subadult mortality (67% j; 21% a; 12% o); $_{\mathrm{M}}$M: maximum subadult mortality (50% j; 40% a; 10% o) and survival ($_{\mathrm{m}}$S: minimum subadult survival (46% j; 35% a; 18% o); $_{\mathrm{M}}$S: maximum subadult survival (50% j; 41% a; 9% o)) profiles for populations of *Rupicapra pyrenaica* are included. Left ternary diagram A, mortality areas are defined by Stiner (1990), U-shaped region (green area) for diachronic or attritional mortality profiles, L-shaped region (blue area) for profiles of catastrophic mortality or for living population structures, J for mortality profiles dominated by juvenile individuals, P for mortality profiles dominated by adult individuals, and O for mortality profiles dominated by senescent individuals. Right ternary diagram B, mortality areas are defined by Discamps & Costamagno (2015), JPO for living or catastrophic profiles, JOP for diachronic profiles, P (pink area) for mortality profiles dominated by adult individuals, and O (yellow area) for mortality profiles dominated by senescent individuals.

Table 2. Life table reconstruction and demographic parameters of the *Rupicapra pyrenaica* population from Valdegoba site. All the fecundity values m_x are inferred from different references and database (Crampe *et al.* 2004; Jones *et al.* 2009; Pérez-Barbería *et al.* 2010). Each parameter and calculation with formulas are detailed in the text. *Lambda (λ) and damping ratio (ρ) calculated with Leslie-Lewis matrices projections from the software R, Version 4.1.0, package 'popbio' (see also text for details).

Age $_{(x)}$	l_x	d_x	q_x	s_x	m_x	$l_x m_x$	T	**Results**
0	1.000	0.143	0.143	0.857	0.000	0.000	0.000	
1	0.857	0.045	0.052	0.948	0.000	0.000	0.000	
2	0.813	0.054	0.066	0.934	0.000	0.000	0.000	
3	0.759	0.054	0.071	0.929	0.156	0.118	0.355	
4	0.705	0.080	0.114	0.886	0.400	0.282	1.129	
5	0.625	0.098	0.157	0.843	0.400	0.250	1.250	
6	0.527	0.036	0.068	0.932	0.400	0.211	1.264	
7	0.491	0.063	0.127	0.873	0.400	0.196	1.375	
8	0.429	0.098	0.229	0.771	0.400	0.171	1.371	
9	0.330	0.036	0.108	0.892	0.400	0.132	1.189	
10	0.295	0.027	0.091	0.909	0.400	0.118	1.179	
11	0.268	0.063	0.233	0.767	0.200	0.054	0.589	
12	0.205	0.054	0.261	0.739	0.200	0.041	0.493	
13	0.152	0.054	0.353	0.647	0.000	0.000	0.000	
14	0.098	0.045	0.455	0.545	0.000	0.000	0.000	
15	0.054	0.036	0.667	0.333	0.000	0.000	0.000	
16	0.018	0.009	0.500	0.500	0.000	0.000	0.000	
17	0.009	0.009	1.000	0.000	0.000	0.000	0.000	
Average			0.26	0.74	0.19			
Total		1.000	4.694	13.306	3.356	1.574	10.194	
Net reproductive rate (R_0)								1.574
Mean generation time (T)								6.478
Lambda or asymptotic growth rate (λ)*								1.075
Damping ratio (ρ)*								1.301

projection in time was applied with the Leslie-Lewis matrices model to determine the asymptotic growth rate (λ) because all the females won't reach the maximum longevity. In Valdegoba the matrices return $\lambda = 1.08$ when population is stabilized (Table 2). Given that the lambda is the ratio of the population size in one year relative to that in the preceding year, the entire population of Valdegoba will increase by about 8% per year, a value within the range observed for populations in the Cantabrian Mountain Range (between 4.7% and 9.6% per year) (Nores & González-Quirós 2009). Once again, our results are similar between Valdegoba and the current Pyrenean *R. pyrenaica* ($\lambda = 1.08$) indicating growing population as well as for the French Alps *R. rupicapra* with $\lambda = 1.04$ (Table S2). The New Zealand *R. rupicapra* being at a perfect equilibrium with $\lambda = 1.00$ (Table S2C).

As mentioned previously, the early fluctuations of λ are known as the transient dynamics: the quicker the fluctuations, the larger the damping ratio (ρ) for a species to converge to age stable distribution. In Valdegoba, the damping ratio ($\rho = 1.30$) indicates that the population converges very quickly to a stable age distribution ($\lambda = 1.08$) around the time step projection t_{12} (Fig. 4). This is also the case for *R. pyrenaica* (French Pyrenees) and *R. rupicapra* (French Alps) reaching their asymptotic regime around t_{16} respectively with $\rho = 1.25$ and $\rho = 1.24$. Finally, there is absolutely no fluctuations for New Zealand chamois showing perfect stable and stationary population and consequently the highest damping ratio $\rho = 1.55$ (Fig. 4, Table S2).

With regard to physical characteristics, the estimated mass of the adult specimens (Table S1) reflects that the average value of Valdegoba's population was 35.49 kg (sd = 8.03), with specimens presenting a maximum value of 53.10 kg and a minimum of 10.71 kg. This average value for the adult individuals allows us to infer the mass and proportion of individuals of each age class following the approach of Zullinger *et al.* (1984), with an estimated mean mass of 31.65 kg for this population (Table 3).

Comparison with other chamois populations

In order to assess the biological and demographics characteristics of Valdegoba's chamois, we compared them with those of current chamois populations. The Valdegoba's profile is very similar with the one of *R. rupicapra* from New Zealand (Caughley 1970; Fig. 2), although the latter population was introduced and may present different characteristics to those of

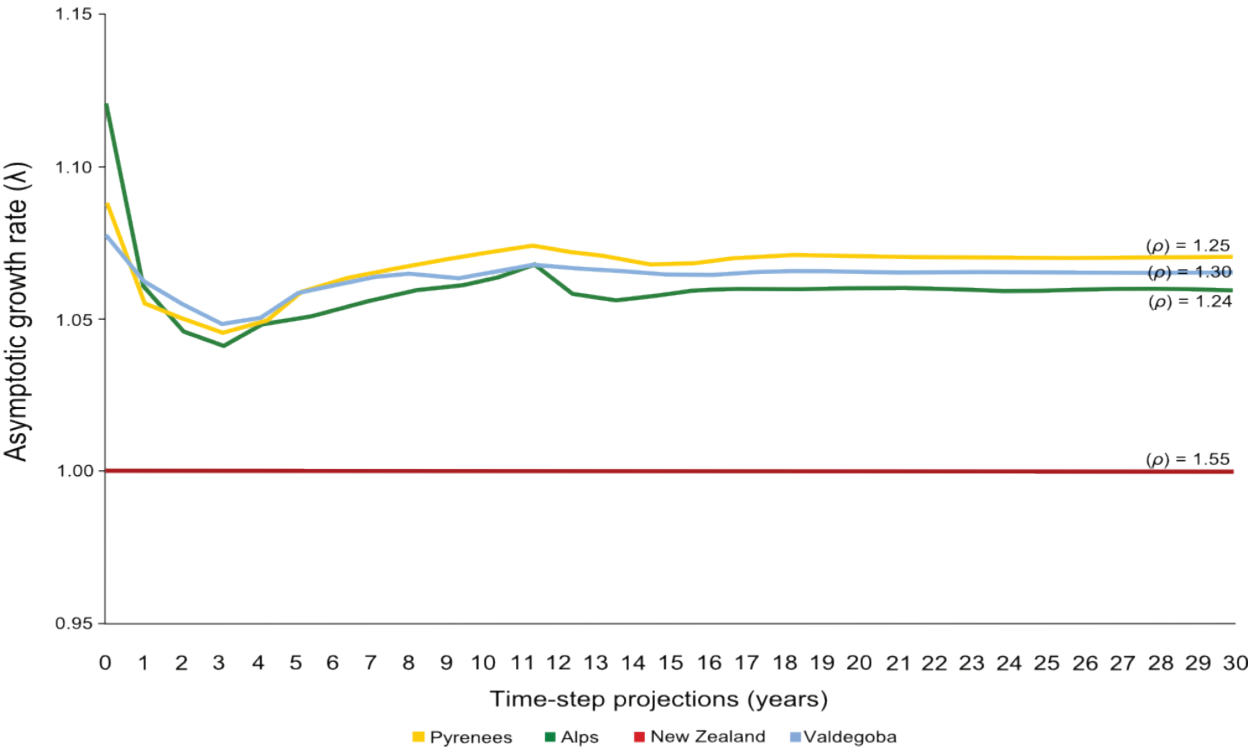

Fig. 4. Time-step projections (year) of the asymptotic growth rate (λ) and the damping ratio (ρ) for the different populations of *Rupicapra* considered in this study. Projections of (λ) are calculated from the Leslie-Lewis matrices outputs with the software PopTools (Hood, 2010 Version 3.2.3.). The calculation of (ρ) was made using the software R (version 4.1.0) and the package 'popbio'.

Table 3. Estimations of average body mass (kg) of the population from biomass values for each age interval, obtained from body size and the proportion of individuals in each age interval (R_x).

Age interval	**Body mass (kg)**	R_x	**Biomass per age interval (kg)**
0	13.05	0.131	1.71
1	28.68	0.112	3.22
2	34.36	0.106	3.66
3	35.32	0.099	3.51
4	35.47	0.092	3.28
5	35.49	0.082	2.91
6	35.49	0.069	2.45
7	35.49	0.064	2.28
8	35.49	0.056	1.99
9	35.49	0.043	1.54
10	35.49	0.039	1.37
11	35.49	0.035	1.25
12	35.49	0.027	0.95
13	35.49	0.020	0.71
14	35.49	0.013	0.46
15	35.49	0.007	0.25
16	35.49	0.002	0.08
17	35.49	0.001	0.04
			Mean = 31.65

the same species located in Europe, such as longevity (10 years in New Zealand but often more than 17 years on average in Europe) (Jones *et al.* 2009; Magalhães & Costa 2009; Myers *et al.* 2020). For this reason, the age phases (juveniles, prime adults, old) do not coincide exactly between all populations. For example, the chamois from the Pyrenees and the Alps show mortality peaks at the beginning of the senescent phase (classes 11–13) (Crampe 1992; Loison *et al.* 1999; Gonzalez & Crampe 2001; Loison 2004), the age

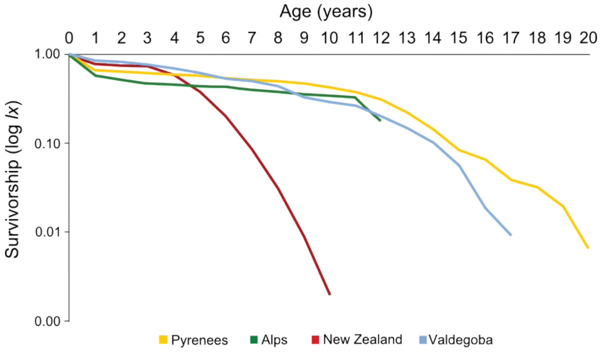

Fig. 5. Survivorship (log l_x) of the current populations of chamois from the French Pyrenees (Crampe, 1992), French Alps Mountains (Loison *et al.*, 1994) and New Zealand (Caughley, 1970), compared to the Valdegoba's fossil population. Data from Table 2 and S2.

interval 9 being the last for the New Zealand population (Fig. 2). According to these profiles, Valdegoba's population is the one that presents the least differences between classes 0 and 1, and the smallest number of individuals in the juvenile phase (between 0 and 36 months).

Only long-term studies of a large sample of marked individuals can detect variation in survival (and consequently mortality) of large herbivores (Gaillard 1998). In our study all the current populations of *Rupicapra* used for comparison were followed for many years providing reliable source for demographic parameters. We will retain here that the average survival s_x (0.76) and the average mortality q_x (0.24) of *R. pyrenaica* from the French Pyrenees (Crampe 1992) are very similar to those recorded for the same species in Valdegoba (0.74 and 0.26, respectively) (Table 2 and S2). Furthermore, despite the lower longevity of the New Zealand population and whatever the species, the Figure 5 shows the typical half-bell shape of the survival curves for large mammals even if there are exceptions to this general pattern (Deevey 1947). This reflects the remarkable property of the Type I mammals survivorship curve (log l_x) with few numbers of offspring, low juvenile mortality and most individuals living to old age. It is opposed to Type II with greatest mortality among the youngest individuals where the survivors are decreasing in a linear and regular way (i.e., birds), whereas the Type III with an 'L' profile shows survival rates that are lower than in the type I and II during the entire lifetime (i.e., fish, invertebrates, plants) (Ricklefs & Miller 1999; Fernandez *et al.* 2006).

The main demographic parameters from each population (R_0, T, λ and ρ, in Table 2 and S2) were used to perform a hierarchical clustering with the popular Ward's minimum variance method (Fig. 6; see details in Ward 1963). The results clearly confirmed the very close proximity between *R. pyrenaica* from Valdegoba and the current chamois population from the Pyrenees and in a lesser extent with the French Alpine *R. rupicapra*. The chamois population from New Zealand is clearly individualized from all the other populations in the clustering analysis.

We performed an ANOVA test for survival and mortality rates for the four populations and significant differences between the means were not found (p = 0.0702). However, when compared by pairs of populations with the Fisher's Least Significant Different (LSD) test, we observed significant differences between the survival and mortality rates of the New Zealand population and those of the Pyrenees and the Alps. Valdegoba's values are closer to those of the Pyrenees and Alps, but no significant differences are observed with New Zealand. A Kruskal Wallis test (K = 9.222) shows significant differences between the medians of the four populations (p-value = 0.026), both for survival and mortality rates, parameters that are interrelated ($s_x + q_x = 1$). When comparing the paired survival rate curves, significant differences are observed between the New Zealand and Valdegoba populations with that of the Alps according to the Kolmogorov-Smirnov test (p = 0.01 and p = 0.022, respectively). These results indicate that, on the one hand, Valdegoba presents similar survival and mortality profiles to those registered in the Alps and Pyrenees, but also with those of New Zealand, on the other hand.

When we plot the four populations age structures into a ternary diagram (Fig. 3), we observe that the profile of the current French Southern chamois is the closest to the Valdegoba chamois, followed by the current French Alpine population. These three populations show an L-shaped profile according to Stiner (1990). In contrast, the mortality pattern of the New Zealand *R. rupicapra* is distributed in the U-shaped region of the diagram, despite being a living population. According to the ternary diagram of Stiner (1990), the four stationary and stable age structures

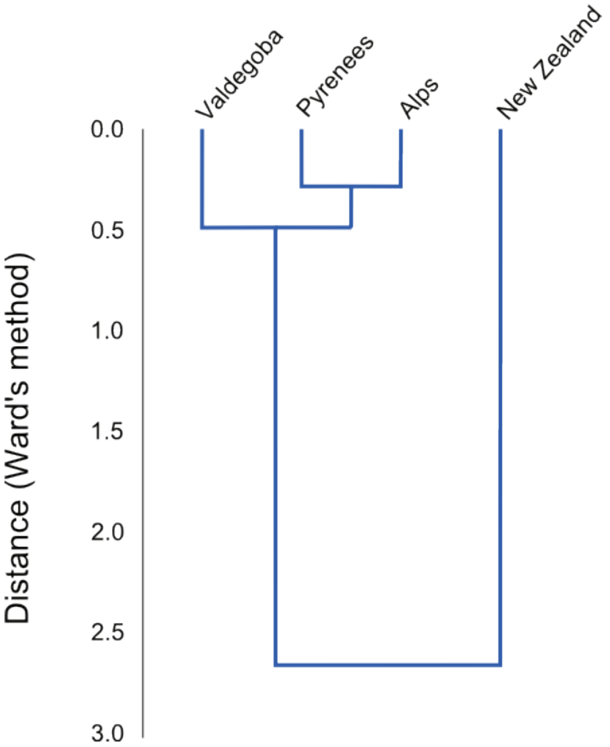

Fig. 6. Hierarchical clustering between different populations of *Rupicapra* considered in this study. Calculation from the demographic parameters (R_0, T, λ, ρ in Table 2 and S2) using Ward's algorithm with the software PAST (Version 3.23) developed by Hammer *et al.* (2001).

($_{M}M$, $_{m}M$, $_{m}S$, and $_{M}S$) obtained using the methodology of Martín-González *et al.* (2016, 2019) should appear located in the U-shaped region. If we consider the regions of the ternary diagram of Discamps & Costamagno (2015), the four structures should appear in the JPO region for living or catastrophic profiles, as occurs in the populations of Valdegoba, Pyrenees and Alps. However, unlike the Valdegoba, Pyrenees and Alps populations, the stable and stationary structures present a higher number of juveniles and a lower abundance of senescent individuals.

Discussion

Population dynamics, theoretical tools and modelling have become key issues in our field for a better understanding of the consequences of environmental variation including carnivore predation and anthropic impact. The starting point of this analysis was to test if the remains of the chamois preserved in Valdegoba showed significant taphonomic biases and to infer palaeodemographic parameters as this ungulate was the prey most intensively exploited by Neanderthals. The results indicated that Valdegoba's fossil record comprises a population where all age intervals are represented (Fig. 2), from kid to senescent individuals, reaching a maximum longevity of 18 years. The chamois from Valdegoba has a good preservation completeness (around 79%) (see Material and methods section), which makes it possible to reliably analyse the fossil population. Based on its mortality profile, which is composed of 24% of juveniles, 46% of prime adults and 30% of old individuals, the death pattern of Valdegoba corresponds either to a catastrophic or to a living population, as suggested by the ternary diagram from both the L-shaped area according to the model of Stiner (1990) and the JPO zone from Discamps & Costamagno (2015; Fig. 3). Thus, assuming the same physiological characteristics (e.g. fecundity, survival), it is very likely that the fossil *R. pyrenaica* that inhabited surroundings of Valdegoba also showed a mortality pattern similar to that found in the cave. It was therefore possible to infer the vital statistics of this population using life tables (Table 2). Moreover, given the absence of an U-shaped mortality curve in Valdegoba, we can discard that the hominins, the main accumulating agent at the site, selectively preyed on very young or on very old individuals.

The demographic parameters of *R. pyrenaica* from Valdegoba are very similar between the moderns Southern chamois (Crampe 1992) and the Alpine one (Loison *et al.* 1994), but all quite different from those of *R. rupicapra* introduced in 1907 in New Zealand (Caughley 1970) (see Results section). The adult survival rates in Valdegoba, in the Pyrenees as well as in the Alps, are high and constant during almost entire lifetime, with only decreasing rates in the very last 2 or 3 age intervals (Table 2). On the contrary the survival of individuals significantly decreases at mid-life in New Zealand population implying shorter mean time generation. If we cannot totally rule out the possibility of a sampling bias (see Caughley 1970), for Loison *et al.* (1994) the lower survival of adults in New Zealand could be explained by the recent introduction of the population and the status of the stationary population. On the contrary, native populations are more likely to increase with high adult survival, larger mean time generation, important net reproductive growth rate and asymptotic growth rate higher than 1 as is the case with Rupicaprini from Valdegoba, the Pyrenees and the Alps.

We should keep in mind that demographic parameters of mammal populations strongly depend on environmental changes through time (e.g. climate, resources, species interactions, etc.) that's why populations merely continue to approach a stable state indefinitely (Stott *et al.* 2011). Therefore, as most populations in the wild are not at equilibrium, transient dynamics with damping ratio are crucial for understanding ecological and life-history dynamics. For example, following hunting cessation, a managed population of red deer (*Cervus elaphus*) on the Isle of Rum (Scotland, UK) showed prolonged transient fluctuations (Coulson *et al.* 2004). This is clearly not the case for the chamois of Valdegoba as well as for the different populations of *Rupicapra* considered in this study. On the contrary, the time-step projections that we performed for the asymptotic growth rate (λ) and the damping ratio (ρ) clearly indicated very short fluctuations through time (Fig. 4). In addition, thank to six metrics of transient dynamics it has been shown that right after a disturbance, mammalian species with a long generation time (i.e., species with a late maturity, a low fecundity, and a long-life span) decrease in population size which is the opposite for the species with a short generation time (Gamelon *et al.* 2014). In our study, there is no such perceptible changes, even if the mean generation time in New Zealand is about twice as small as the one reported for Valdegoba as well as for the other modern populations. Our results argue that the Valdegoba population was able to sustain continuous exploitation of different cohorts by Neanderthals through time without collapsing.

In addition, our results also provide interesting clues for this study. Firstly, the comparison of life tables between the fossil population of Valdegoba with extant Rupicaprini confirm the very good preservation conditions in the Spanish cave as well as a rich and little biased fossil record. Our study delivers unique palaeodemographic information of similar quality to that obtained from the extant populations analysed. Secondly, from a taphonomic point of view, we have reported in Valdegoba a possible difference in treatment between chamois depending on their age. This allows us to discuss mortality profiles derived from extinct populations with similar age structures. Compared with the four population profiles modelled in this work with stationary and stability conditions (${}_{M}$M, ${}_{m}$M, ${}_{m}$S, and ${}_{M}$S) (see Material and methods section), the population of Valdegoba shows the least differences in number of individuals between age intervals 1 and 2, as well as the lowest number of individuals in whole juvenile phase, where no significant sampling bias was identified (see Fryxell 1986). These differences in the composition of juvenile individuals with respect to structures with stable and stationary conditions may be due to the size of the prey and their fossilization capabilities, since body size is one of the factors with greater influence on the potential preservation of skeletal remains (Behrensmeyer *et al.* 1979; Behrensmeyer & Dechant-Boaz 1980; Damuth 1982). In the case of the cranial and postcranial bones, this explains the lower preservation completeness of the record of juvenile individuals compared to adults. However, in this study we used tooth specimens for estimating the abundance of individuals by age intervals, and teeth are usually the remains with greater fossilization potential. For this reason, no significant biases affecting the quantitative representation of different age phases should be expected. In this way, the low frequencies observed for the juvenile phase of the chamois population of Valdegoba compared to the living populations could be attributed to a lower preference of Neanderthals for these individuals, which provided less flesh and within-bone nutrients. Moreover, another factor that could explain this difference is that the carcasses of juvenile individuals might not have been transported to the site to the same extent as those of adults given their lower nutritional value. This hypothesis is similar to the one proposed in the Early Pleistocene site of Venta Micena (Spain) which was probably lying in the surroundings of a den of the large hyaenid *Pachycrocuta brevirostris*, where small sized ungulates are underrepresented (Arribas & Palmqvist 1998; Palmqvist & Arribas 2001). If such interpretation holds, it means that the carcasses of kids, yearlings and other subadults would be completely consumed at the kill site, while those of adults would be transported for processing at the site thanks to their higher nutritional value. The interpretation of a lower preference for the transport of juveniles might be supported by the proportion of individuals in each age interval (Fig. 5), which shows a smoother profile curve for Valdegoba than in the other populations, with less pronounced changes between the three age phases (i.e., juveniles, prime and old adults). However, at Misliya (Yeshurun *et al.* 2007), the transport of whole mountain gazelle individuals is observed, weighing around 20kg, which is lower than the average mass of chamois juveniles at Valdegoba (see Table 3). Therefore, this distribution could basically reflect that Neanderthals had a greater preference for adults and senescent individuals than for juveniles, as observed in other sites with Neanderthal activity (e.g. Gaudzinski & Roebroeks 2000; Hoffecker & Cleghorn 2000; Valensi & Psathi 2004; Alder *et al.* 2006). This trend differs from those present in modern chamois populations, in which a more pronounced downward slope can be seen in the juvenile and senescent phases, while a less pronounced one is found for adults (Fig. 5). The less steep the slope, the fewer deaths occur during shifts in age class. Finally, another aspect we should consider is the group behaviour of chamois. In her analysis of the population of the National Game Reserve of Orlu in the Eastern French Pyrenees chamois, Loison (1999) noted a tendency for males between 2 and 4 years of age to disperse and appear underrepresented in the samples, which may have influenced the recording of the Valdegoba population.

With regard to the discussion on mortality or survival profiles for stable and stationary populations, it is interesting to note that the ${}_{m}$S (minimum survival) and ${}_{M}$M (maximum mortality) structures almost overlap (Fig. 3). This suggests that perhaps the taphonomic record may not allow differentiation between death or living profiles in those populations that meet stable and stationary conditions. This is important when we are aimed to reconstruct the life table of a population from the specimens found in a deposit, as in this study. If the proportions of individuals in each age category cannot be differentiated, it is necessary to rely on other disciplines for understanding how the assemblage was formed. Based on the results with stable and stationary age structures, we could have two populations of quite different taphonomic origin that could generate similar ternary diagrams, for example a population with asynchronous mortality, in which the individuals were killed with the same probability in all age intervals, and another in which the deaths took place synchronously due to a natural disaster, such as a flooding. Therefore, another interesting question for future work will be to explore in further depth whether stable and stationary populations of other species also cover the region of the ternary diagram of Discamps & Costamagno (2015), where the chamois population of Valdegoba is located.

From our point of view, an interesting contribution of our analysis is that it allows deducing demographic difference among the populations. This is the case for the chamois from New Zealand, which shows a population profile similar in shape to the Pyrenees but with a shorter longevity. According to the data shown in Figure 5, we could suggest that the phase of prime adults in New Zealand does not exceed 4 years, while that for Pyrenees reaches 10 years. This assumption can be complemented with the analysis of ternary diagrams (Fig. 3), which shows that the populations of Valdegoba, Pyrenees and Alps are in the L-shaped region of Stiner (1990), but the one of New Zealand is in the U-shaped region, in spite of the fact that it is a living population. This may result from differences in the biological characteristics of the first three populations compared to that of New Zealand (see Caughley 1970; Crampe 1997; Pérez-Barbería *et al.* 1998; Pérez-Barbería *et al.* 2010). For this reason, in order to correctly represent the latter population in the ternary diagram of Discamps & Costamagno (2015), the juvenile and prime adult phases would need to be reduced. Furthermore, based on the previous study of Caughley (1970), Loison *et al.* (1994) proposed that these differences may mainly be due to intrinsic demographic characteristics or methodological and sampling biases.

Besides the palaeodemographic analysis of the population structure and the values of the life table, the results of this study provide an estimate of the average mass of the chamois population of Valdegoba of 31.65 kg (Table 3). This body mass is slightly higher than in the living populations, where the adult body mass is estimated between 22 and 30 kg (Herrero *et al.* 1998; Pérez-Barbería *et al.* 2010). It is not possible to differentiate between males and females in these estimates, because bimodal distribution is not observed. However, an osteological analysis of sexual dimorphism in Valdegoba showed differences between males and females, as the males had larger dimensions than those of the living populations, which agrees with our mass estimates, while the females had a similar size (Arceredillo *et al.* 2011). In modern populations of *Rupicapra* there are not intersexual differences in body mass at high density levels (Couilloud *et al.* 1999; Pépin *et al.* 1996). This could suggest that the population of Valdegoba did not reach its maximum density. In addition to population density, sexual dimorphism can be used as a bioindicator of other biological parameters of the chamois (see Pérez-Barbería & Palacios 2009).

Although there are few Middle Palaeolithic sites where the most represented species is chamois, it should be noted that the processing and consumption of Southern chamois by Neanderthals was predominant in Valdegoba, followed by horse meat, with defleshing being the main butchering activity in the site (see Díez 2006). The body mass estimates of chamois obtained in this study makes it arguable how this prey was exploited by Neanderthals. According to the proposal of Viljoen (1993) (based on the works of Ledger 1968; von La Chevallerie 1970), the extractable biomass of the chamois bodies would be around 80% of its body mass, which is the percentage assigned for species of <50 kg. For *R. rupicapra* in the Italian peninsula, Ramanzin *et al.* (2010) used 83%. However, in White's (1953) estimates for different species, none of them reached >70%, although he did not show values for species similar in size to *R. pyrenaica*. Taking the above into account, a percentage of 80% could be applied to the mass of dead individuals for each size class to understand how much biomass could be extracted and used by the Neanderthals. Therefore, according to the mean mass value of the population (31.65 kg), 80% of this mass would mean that the Neanderthals had access to an average of 25.32 kg of meat resources from each individual.

In order to understand how much energy can be extracted from the proportion of usable matter, it is necessary to know the body composition of the chamois, but this information is scarce (Ramanzin *et al.* 2010). The composition of the meat loin of *R. rupicapra* has an average water content of 75.1%, 22.8% of protein and 0.9% of fat (Hofbauer *et al.* 2006), although it is worth noting that there are significant variations in the body composition of chamois as a function of population age, hunting season, sex, and physiological condition (e.g. McCormick 2003; Hofbauer *et al.* 2006; Ramanzin *et al.* 2010; Flores-Saavedra *et al.* 2018). If the values listed above are used as a mean of the population and a conversion factor of 4.27 for protein and 9.02 for fat is used, as suggested by the United States Department of Agriculture (USDA), 100 g of *R. rupicapra* meat would provide 105.1 kcal. This estimate is close to the one obtained for goats (109 kcal/100 g), although the latter have a higher percentage of fat (2.31%) (USDA). Given that in this analysis we consider the same body composition between *R. pyrenaica* and of *R. rupicapra*, a conversion factor of 105.1 kcal/100 g would represent the potential energy to which Neanderthals could have access from the Southern chamois individuals. Considering this conversion factor and 25.32 kg extracted from each Southern chamois carcass (see above), means that each carcass could provide 26,608 kcal. Marrow and grease are considered a relevant nutritional source for Pleistocene humans (e.g. Blasco 2019; Espigares *et al.* 2019). However, Díez (2006) observes that among the activities carried out by humans on small-sized species in Valdegoba, including chamois, access to grease and marrow only accounts for 0.9%, which leads us to consider that it was a marginal activity. For medium-sized species this percentage increases to 1.3%, and for large species it is not observed. Given this information, we understand that these resources were not exploited by the humans of Cave of Valdegoba, and we do not consider them as energy that could be obtained from the chamois.

In addition to the biomass and extractable energy of the chamois, in order to understand the relationship of Neanderthals with this species it is necessary to know what the actual demand for meat of these hominins. Currently, this is a subject of debate and of important scientific production (e.g. Sorensen &Leonard 2001; Steegmann *et al.* 2002; Churchill 2006; Snodgrass & Leonard 2009; Mateos *et al.* 2014; Venner 2018). Venner (2018) proposed in a recent study a value of energy demands for adult Neanderthals of around 3,450 kcal/day, which was obtained after refining previous methodologies that estimated energy demands between 2,870 and 6,754 kcal/day (Sorensen & Leonard 2001; Steegmann *et al.* 2002; Churchill 2006; Snodgrass & Leonard 2009). This estimate is above the 2,200-2,900 kcal/day reported for some modern hunter-gatherer populations (Eaton *et al.* 1997), but close to that of Siberian Yakuts when moderate physical activity is considered (≈3,200 kcal/day) (Venner 2018). In most modern hunter-gatherer populations, it is observed that the consumption of animal resources represents between 30 and 60% of their dietary intake (Jenike 2001; Leonard *et al.* 2007). However, it has been argued that the percentage of meat in the diet of Neanderthals could be higher. According to a study of dental micro-wear, El Zaatari *et al.* (2011) suggested the Neanderthals inhabiting in open environments had a meat consumption above 85% of their diet, like the Fuegians from Tierra de Fuego (Argentina) (e.g. Bridges 1885; Murdock 1962), whereas those from woodland environments would have a plant consumption similar to the Chumash, between 36 and 46% of their diet (which correspond to between 64 and 54% of meat, respectively) (Murdock 1964). On the other hand, El Zaatari *et al.* (2011) proposed a high plant content in the diet of the Neanderthal population of Monsempron 3, because they showed a pattern of tooth microwear closer to the Khoe-San hunter-gatherers, whose diets include a plant content between 60 and 80% (e.g. Lee 1979; Silberbauer 1981).

Given that the study that provides more information on the environment of the Valdegoba site shows a mixed one (Feranec *et al.* 2010), an average of meat consumption between the percentages of the Fuegians and the Chumash, 72% is assumed in this study. If we consider this percentage for the Neanderthals of Valdegoba and the estimate of daily energy expenditure provided by Venner (2018), meat consumption would represent around 2,484 kcal/day. Given that the chamois remains represent approximately 58% of the fossil sample unearthed in the cave, it can be considered that the consumption of this species would correspond to 1,441 kcal/day. We contemplate that this assumption can be made due to the predominant consumption of Southern chamois in Valdegoba throughout the year by Neanderthals, but we know that they used a wide variety of animal resource, avoiding a specialist or dependence relationship on this elusive species (see Díez 2006). Considering that of each chamois could be extracted 25.32 kg and 26,608 kcal (see above), one carcass provided enough meat to supply the meat demand of 18.46 adult individuals (10.71 adult individuals if the total percentage of daily meat was supplied by this bovid). Based on the fossil record of other Middle Palaeolithic sites in the region, in which the most common meat resources are red deer (*Cervus elaphus*) or horses (*Equus ferus*) (e.g. Altuna 1972; Moure Romanillo & García-Soto 1983; Torres *et al.* 1989; Castaños Ugarte 2005; Navazo *et al.* 2005), we are also aware that the exploitation of Southern chamois at Valdegoba seems to be more of an exception than a rule. For this reason, our calculations are specific to this site and its characteristics and cannot be directly extrapolated to other sites with other conditions and interpretations.

In modern hunter-gatherer populations, optimal group size is set to 30 individuals (Marlowe 2005). If we assume that Neanderthals had a similar group size, their demand for chamois meat would be approximately 43,230 kcal/day (1,441kcal/day * 30 individuals), i.e., 1.62 chamois per day. We understand that this is an overestimation of the dietary demands of this human group, as a considerable part of the group would be sub-adult individuals, with less energy demands. Thus, it is reasonable that the 18.46 adult individuals that a chamois would be equivalent to the demands of a population of 30 individuals of different ages. Further work would be required to refine this approximation to have more precise energy requirement values of the group. Nonetheless, this assumption implies that the group would need between 365 and 593 chamois annually. Currently, the maximum density of chamois in the Cantabrian coast is 23 individuals per km^2 (Pérez-Barbería & Palacios 2009). If this value represents the one found in the environment surrounding Valdegoba, the Neanderthals would have had to exploit at least between 16 and 25 km^2, but it must be considered that they possibly had to exploit considerably larger areas. On one hand, it is highly probable that the density values were not homogeneous throughout the space; furthermore, as previously discussed, evidence from sexual dimorphism analysis suggested that the Valdegoba's population did not reach its maximum density (Arceredillo *et al.* 2011; Couilloud *et al.* 1999; Pépin *et al.* 1996). On the other hand, a maximum density of 23 individuals per km^2 would correspond to the living individuals of the entire population. If Neanderthals consumed all individuals from nearby populations, they would have had to exploit more and more distant regions, being forced to move to other places of residence. For these reasons, it is considered that they would have to exploit areas considerably larger than 26 km^2 per year.

According to the average survival rate of chamois in Valdegoba, 74% of individuals of each age class would survive. If this approach is used for the total population of chamois, in a population reaching the maximum density of 23 individuals per km^2 this means that ≈ 17 individuals would survive and ≈ 6 would die. With these values, the Neanderthals would need to exploit between 60.8 and 98.8 km^2 annually if the chamois populations presented a similar maximum density. Applying our results to regions close to Valdegoba Cave that may have been exploited by Neanderthal groups, we can find sites where Southern chamois have been recorded during the Middle Palaeolithic, but with lower presence than in Valdegoba, such as: Prado Vargas, Cueva Millán, La Ermita, and Arrillor (Moure Romanillo & García-Soto 1983; Torres *et al.* 1989; Moure Romanillo *et al.* 1997; Castaños Ugarte 2005; Navazo *et al.* 2005; Arceredillo 2015; Romero Alonso 2020). The area comprised between these sites is greater than 5,000 km^2. If we consider Southern chamois populations homogeneous and with maximum densities, more than 50 human groups could have inhabited this region. It is interesting to note that the distribution and abundance of chamois during the glaciations of the MIS 4-2 (Würm period) were greater than those observed today, being mainly found at low altitude in the most important mountain systems (Masini 1985; Lovari 1987; Masini & Lovari 1988; Domínguez Sanjurjo *et al.* 2009). This means that the Neanderthals could have been able to exploit this species in an area larger than the one currently occupied by the extant chamois population in the Cantabrian Mountain Range, and this resource could have been more common for the populations of this region in the north of the Iberian Peninsula during the Late Pleistocene. However, Domínguez Sanjurjo *et al.* (2009) suggested that the chamois were displaced at low altitudes during the Würm period because the thermal conditions were a limiting factor for their distribution. Therefore, the chamois would not be found in areas similar to the current ones. This did not occur during the Riss-Würm interglacial period (MIS 5), in which the chamois inhabited high altitudes in the Swiss Alps, as observed in the fossil record of this region (Domínguez Sanjurjo *et al.* 2009).

One aspect that we have not addressed is how Neanderthals obtained the Southern chamois. Although it has been proposed that access to meat by Neanderthals was primarily as scavengers (Binford 1981, 1984; Chase 1989; Stiner 1991, 1994), it is now widely accepted that they did so through hunting (e.g., Scott 1986; Grayson & Delpech 2002; Yravedra & Cobo-Sánchez 2015). Díez (2006) proposed that Neanderthals from Valdegoba would hunt groups of Southern chamois that would be linked to mid-altitude summer-autumn grasslands. The analysis carried out by Yravedra & Cobo-Sánchez (2015) on hunting habits of Neanderthals in Southern Europe has shown that they had a great capacity to adapt to different environments, including mountainous environments, to take prey such as Iberian ibex and Southern chamois. Middle Palaeolithic sites near Valdegoba with presence of Southern chamois such as Cueva Millán, La Ermita, Prado Vargas or Cueva Corazón provide evidence of very diverse origins and complex occupational histories (Navazo *et al.* 2005; Díez *et al.* 2008; Yravedra 2007). Some of these sites are located in internal, mountainous and steep areas, which led Yravedra & Cobo-Sánchez (2015) to argue that Neanderthals would have been adapted to hunting in these ecosystems, as also suggested by Díez (2006) for the Valdegoba population.

In order to gain a deeper understanding of the exploitation of meat resources by Neanderthals in the Valdegoba surroundings, the reconstruction of the food web of the large mammal community will be of interest, since this will allow us to assess the competition with carnivore species for this resource, and whether the interaction with them could have conditioned their continued presence in this region. This could help to interpret the dynamics of the use of the Cave of Valdegoba by humans and carnivore species as observed in its record.

Conclusions

The Valdegoba site has a chamois record of high preservation completeness. There are specimens of chamois representing all age intervals, from juveniles to senescents. The analysis of each age class of Valdegoba's chamois records shows a pattern of mortality close to a living structure, very close to that of modern populations, although with fewer juveniles and more senescent individuals. The palaeodemographic analysis (Leslie-Lewis model) clearly indicates that the Southern chamois from Valdegoba was not affected by the regular consumption of Neanderthals with a stationary and growing population. Furthermore, values from the life tables are closer to those of the Pyrenean population than to the Alps one. However, there are differences in body mass, with Valdegoba's chamois being slightly larger than in the modern populations of the Cantabrian Mountains and the Pyrenees. According to our results, the Neanderthals would have exploited between 61 and 99 km^2, annually, to cover the dietary meat resources that chamois represented for this population. Considering that the chamois populations had greater abundance and a wider distribution during the time period in which Valdegoba was inhabited, compared to the current populations of this species in the Cantabrian Mountain Range, this bovid could have been a recurring resource in the diet of Neanderthals.

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