Revisiting macromammal exploitation in the Spanish Cantabrian region during the lower Magdalenian (*ca.* 20-17 ky cal BP)

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ABSTRACT

Understanding the ways in which human groups use the environment for their survival is one of the main fields of study in Prehistory. Subsistence strategies, understood as the set of techniques, processes and activities through which human groups organise the tasks related to their survival, are a fundamental element for understanding the economic and sociocultural processes derived from these practices in the past. In this sense, archaeozoological and taphonomic studies are the main tool to reconstruct the ways in which our ancestors acquired, processed, consumed, and managed meat resources for their survival. In this research we examine the ways in which hunter-gatherer groups in the Spanish Cantabrian region exploited ungulates through a palaeoecological and palaeoeconomic analysis of a total of 32 archaeological levels at 19 sites dated between 20 and 17 ky cal BP. To this end, through research on faunal resources in this region, we will address the ways in which prey was acquired and transported, the age ranges, the seasonality of the captures and the nutritional energy contribution to the diet of the human groups, taking into account the cost of acquiring them, thus generating an updated view of subsistence strategies in the Cantabrian region.

1. Introduction

The Magdalenian period (ca. 20.5-14 ky cal BP) is dated during the final phases of the Pleistocene, following the Glacial Maximum, in Marine Isotopic Stadial 2, that is, during the Greenland Stadial 2 and Greenland Interstadial 1 (Grootes et al., 1993; Rasmussen et al., 2014). In the Spanish Cantabrian region, it is the Upper Palaeolithic period with the largest number of documented sites. Within this period, the lower Magdalenian (ca. 20-17 ky cal BP) has been documented at about thirty sites, many of which present faunal studies carried out in the last decade. They are located in the valleys of Sella (El Cierro, Cova Rosa and La Güelga) (Álvarez-Fernández et al., 2019, 2022; Portero et al., 2019; Rojo, 2020), Nalón (Las Caldas) (Altuna and Mariezkurrena, 2017), Cares (Arangas and Coímbre B) (Yravedra et al., 2017; Álvarez-Fernández, 2020), Asón (El Mirón) (Carvalho et al., 2021) and Saja rivers (Cualventi, El Linar and Las Aguas) (Castaños, 2016). All

these studies have shown the importance of faunal resources, mainly macromammals, in the diet of lower Magdalenian human groups. The importance of vegetables in subsistence also has been highlighted for this period (Zurro, 2010; Power et al., 2015; Uzquiano, 2019), while other animal resources would be complementary in the diet, such as birds (Elorza, 2014; Rufà et al., 2022) and, in particular, marine vertebrates and invertebrates (Álvarez-Fernández, 2011), at a time when marine regression meant that the coastline was 10 km further away than at present (Thompson and Goldstein, 2006; Jordá Pardo et al., 2018).

Palaeoeconomic studies focused on the exploitation of macromammals in the Cantabrian region began to develop in the 1970s, specifically after the publication of the PhD Thesis of Altuna (1972), which became the main reference for subsequent research. From this work, others began to be developed, based on archaeofaunal resources, which focused on analysing economic forms and hunting strategies as a way of understanding the processes of change and evolution in human

behaviour in prehistoric times. In this way, Freeman (1973) for the first time provided an ecological explanation of cultural changes based on the strategies of animal exploitation from the perspective of processual archaeology. As a result of the large number of red deer remains documented in the sites identified by Altuna (1972), Freeman indicated that the hunting strategy probably centred on the specialised capture of this ungulate during the Magdalenian period. These documented faunas were also used by González-Echegaray (1972–1973) in his explanation of the climatic and environmental changes that occurred during the lower Magdalenian. However, it was Altuna (1979) who pointed out, for the first time, that the hunting strategy at the end of the Upper Palaeolithic in the Cantabrian region followed a dichotomy between sites specialised in red deer hunting and those focused on Iberian ibex, depending on the biotope in which they were located. These approaches made a great impact throughout the 1970s, driven by the development of archaeological excavations at numerous sites, involving multidisciplinary teams and improved archaeological recovery methods (e.g., the use of sieves with finer mesh), which allowed the recovery of small-sized archaeofaunal elements (Altuna, 1976, 1979; Straus, 1977; Álvarez-Fernández, 2011).

In the 1980s, these economic approaches began to be included in several PhD theses focusing on the Cantabrian Magdalenian (Utrilla, 1981; González Sainz, 1989). Other works used faunal elements to explain the economic changes that occurred at the sites from a Marxist point of view (Gómez-Fuentes, 1982, 1983), and even subsistence was analysed from ecological and environmentalist perspectives (Bailey, 1983). Archaeozoological studies in the region also multiplied, motivated by the multitude of archaeological excavations carried out at different sites and the publication of the results in interdisciplinary and multidisciplinary monographs on sites such as La Riera (Altuna, 1986), El Juyo (Klein and Cruz Uribe, 1987), Ekain (Altuna and Mariezkurrena, 1984) and Erralla (Altuna and Mariezkurrena, 1985).

Based on the volume of archaeozoological information generated up to the 1990s, researchers tried to explain the changes in subsistence patterns at regional level from different perspectives. In this sense, the first difficulties arose for the comparative study of subsistence strategies in Magdalenian sites, such as the age of the excavations from which some faunal data came, the system for collecting remains, the need for a common archaeozoological methodology, or the importance of data from radiocarbon-dated levels and analysing strategies from an interdisciplinary point of view (e.g., Altuna, 1990, 1995; González Sainz, 1992; Quesada, 1997).

Environmental studies continued to develop, introducing in some cases analytical variants from a new functionalist perspective. Thus, the first ecological indices began to be applied to explain the specialization or diversification of hunting assemblages (Quesada, 1997); research which, however, was not continued in the following years. This decade also saw the appearance of the first works that included taphonomic aspects in the investigation of faunal materials (e.g., Pumarejo and Bernaldo de Quirós, 1990; Pumarejo and Cabrera, 1992; Mateos, 1999).

The new millennium saw a great advance in the interpretation of subsistence strategies at sites in the Cantabrian region, owing to the development of taphonomic studies based on common methodological criteria (Yravedra, 2000, 2002a, 2002b; Mateos, 2003). This led to many of the sites with old excavations being reviewed from a taphonomic point of view to identify the responsible of bone accumulations (e.g., Yravedra, 2003–2004, 2010; Yravedra et al., 2017). These taphonomic studies showed that hunting strategies were not only subject to ecological processes, and for the first time the concepts of diversification and specialization were questioned and the difficulty of adjusting a theoretical model to the specificities of the Cantabrian region was underlined (Yravedra, 2002a, 2002b). This debate led to a reconsideration of hunting as a phenomenon of specialised and diversified behaviour, which made it necessary to include the particularities of each site and each region through archaeozoological and taphonomic analyses, based on criteria that allow all the variables to be considered.

During the last decades the development of GIS software, together with the improvement of computers, has led to the integration of detailed geographic information from sites in the study of subsistence behaviours, allowing the calculation of the potential distance to faunal resources and the influence of site location, orientation, insolation, and slope on hunting strategies (e.g., Marín, 2010; Andrés-Herrero et al., 2018). Theoretical models from ecology have also been applied, specifically in relation to the Optimal Foraging Theory, which is based on the principle that hunter-gatherers' subsistence behaviour will be aimed at obtaining the maximum energetic yield, and therefore, by studying a number of economically observable parameters - such as the nutritional energy provided by the animals, the time spent hunting and handling them, and the cost of return - it is possible to estimate which prey are the most energetically profitable (MacArthur and Pianka, 1966; Winterhalder, 2001). For the period we address in this paper, these theories have been applied by Marín (2008, 2009).

All this research has greatly advanced our knowledge of the subsistence strategies of lower Magdalenian human groups in the Cantabrian Spain. However, and despite the development of analytical methods, the classic picture proposed in the 1980s that hunting depended on the biotope in which the site is located has remained broadly the same, with some nuances established in subsequent decades in connection with particular sites (e.g., González Sainz, 1992; Yravedra, 2002a, 2002b; Marín, 2010; Portero et al., 2019, Portero, 2022).

In summary, and following the proposed theoretical models, we can distinguish three types of sites based on the location and faunal spectrum of the remains (González Sainz, 1992):

1. A coastal model, with a significant predominance of red deer in the sequence. This applies to sites located in valley areas close to the coast, where this species would be very abundant.
2. A mountain model, with sequences showing high percentages of crag animals (Iberian ibex and chamois). This corresponds to sites located in mountainous or steeply sloping areas.
3. An inland valley model, in which the proximity to different biotopes allows the exploitation of several ecosystems, resulting in greater diversification in the faunal spectrum at the sites.

Considering these models and combining palaeoecological and palaeoeconomic analyses of lower Magdalenian sites, in this paper we approach the subsistence strategies carried out by Magdalenian groups in the Spanish Cantabrian region taking into account the aspects discussed above and trying to relate as many elements as possible that may have influenced the subsistence of those groups. In this way an updated view will be obtained for the exploitation of macromammals in this region between ca. 20 and 17 ky cal BP. The results obtained have highlighted the important role that the red deer had in the diet, being the most hunted prey and providing the greatest amount of calories to the Magdalenian human groups of the Cantabrian region.

2. Materials and methods

2.1. Lower Magdalenian sites in the Spanish Cantabrian region

The faunal information analysed for this territory during the lower Magdalenian comes from different studies carried out at different times and with very different methodologies. To ensure that comparisons of subsistence strategies are founded on the same analytical basis, we have selected the levels at archaeological sites that meet the following criteria:

2.1.1. Radiocarbon-dated levels

To establish a chronological framework on which to make these comparisons, it is necessary that the levels from which the faunal remains come have radiocarbon dates. We have excluded from the study those levels whose dates have problems of cultural ascription, have been

discarded by researchers because they are discordant with those obtained in the archaeological record, or have a standard deviation that prevents them from being correctly placed in their chronological and cultural framework (e.g. Juyo 6 or Riera 20).

To unify the chronological information, we have calibrated all the radiocarbon dates of the selected levels with the OxCal 4.4. program (Bronk Ramsey, 2009) and the IntCal20 calibration curve (Reimer et al., 2020) for terrestrial samples, and the Marine20 curve (Heaton et al., 2020) for samples of marine origin. In the latter case, the marine reservoir effect for the Cantabrian Sea has been included, which gives a Delta ± R of −117 ± 70 for the end of the Pleistocene (Monge Soares et al., 2016). Thus, all dates have received the same calibration treatment. In this article, new radiocarbon dates have been included for some contexts dated decades ago, to better specify their occupations (Las Caldas and La Güelga), as well as for sites excavated in the last century, where recent archaeozoological studies have been carried out (El Cierro) (Appendix 1, Table 1).

2.1.2. Faunal remains from excavations carried out with modern recovery techniques

To avoid biases in the anatomical and taxonomic representation of the documented species due to the age of the excavations and excavation methods, we have only selected levels at sites where excavations were carried out from the 1970s onwards, when modern methods of archaeological excavation became widespread in the Cantabrian region (Álvarez-Fernández, 2011; Portero et al., 2019). That is, systems based on stratigraphic principles that make it possible to determine the accuracy and origin of the provenance of the finds while integrating precise recovery of the material by means of sieving with different mesh sizes (Ruíz Zapatero, 2013). This criterion excludes some sites, such as La Paloma (Asturias), Cueva Morín (Cantabria) or Atxeta (Basque Country).

2.1.3. Faunal remains studied by an archaeozoologist

This requirement, that the information comes from methodologically sound archaeozoological studies, is essential for the data to be compared. In addition, the remains from the levels analysed must number at least $n \geq 30$ to be able to make the relevant analytical comparisons.

With these assumptions, we have compared subsistence strategies for a total of 32 stratigraphic levels from 19 sites (Fig. 1).

2.2. Palaeoecological analysis

The palaeoecological study has been carried out using ecological index to measure the richness, abundance and homogeneity of the species present in the ecosystem, helping us to evaluate the specific weight that each of them possess within an archaeological sequence (Magurran, 1988; Grayson and Delpech, 2002; Jones, 2004; Faith and Du, 2018).

Simpson's diversity index (***D***) has been used to evaluate the biodiversity of the archaeological levels, which measures, from a given number of species found in an ecosystem, the relative abundance of each one of them. This index is expressed as follows:

$$D = \sum_{i=1}^{s} \frac{n_i(n_i - 1)}{N(N - 1)}$$

where S is the number of taxa within the assemblage, n_i the number of individuals of a species i, and N the total number of individuals in the community. This index will indicate the differences or similarities of faunal comparisons without being greatly affected by the number of remains, as it is an index that can be used with small samples. We also used Simpson's Reciprocal Index, which consists of dividing 1 by Simpson's index (1/D), and which has been frequently used in zooarchaeological research (e.g., Grayson and Delpech, 2002; Jones, 2004; Faith and Du, 2018; Portero et al., 2022).

Shannon's index (***H′***) has been calculated with the following equation:

$$H = - \sum pi \ ln \ pi$$

where pi is the proportional abundance of i taxon. This index measures the heterogeneity of a community based on the number of species in the sample and the relative abundance of each of them. Although this index has no upper value limit, it usually fluctuates between 0 and 5. This in practice implies that, in highly taxon-dominated assemblages, the value of ***H′*** will be close to 0 (Grayson and Delpech, 2002; Jost, 2010; Portero et al., 2022).

To determine the degree of homogeneity of a faunal assemblage, the Shannon homogeneity index or *Evenness* (***E***) has been calculated with the following equation:

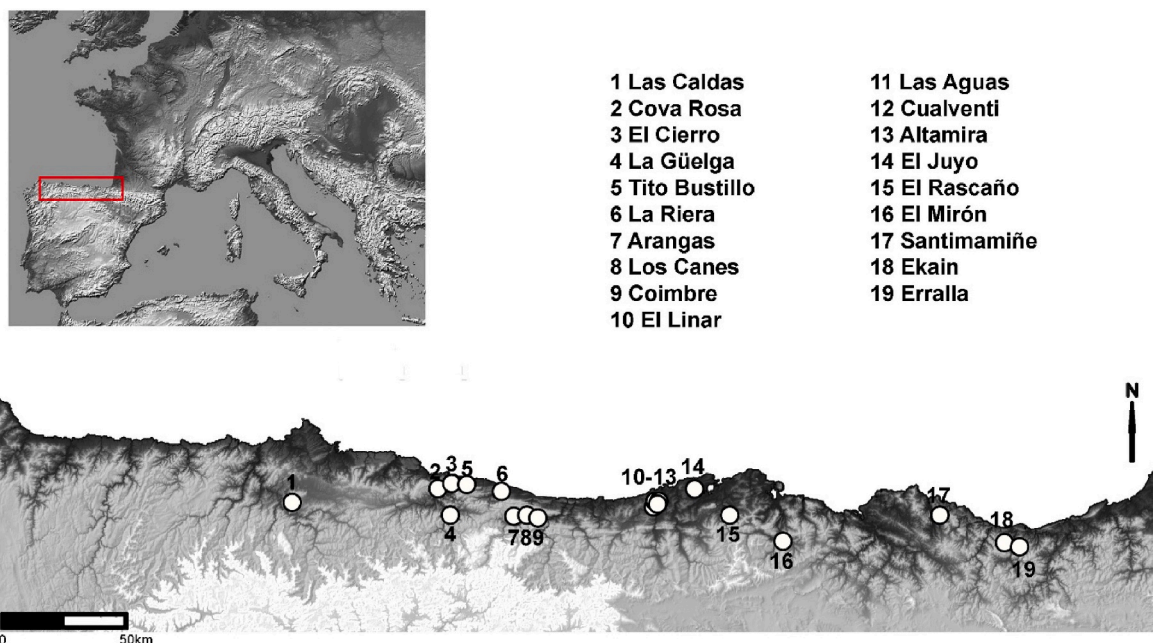|	
1 Las Caldas	11 Las Aguas
2 Cova Rosa	12 Cualventi
3 El Cierro	13 Altamira
4 La Güelga	14 El Juyo
5 Tito Bustillo	15 El Rascaño
6 La Riera	16 El Mirón
7 Arangas	17 Santimamiñe
8 Los Canes	18 Ekain
9 Coimbre	19 Erralla
10 El Linar	

Fig. 1. Map of the sites in the Cantabrian Region with lower Magdalenian occupations selected for the present study.

$$E = -\sum p i \, ln \, p i \Big/ ln \, (S)$$

This index fluctuates between 0 and 1; the closer to 0, the lower the homogeneity (Grayson and Delpech, 2002; Jost, 2010; Faith and Du, 2018).

The Effective Number of Species (***qD***) of the animals in the ecosystem was also analysed using the exponential of Shannon's index:

$$qD = exp\left(-\sum p i \, ln \, p i \right)$$

This configuration allows us to convert diversity indexes into effective numbers, providing an indicator that determines how many species we can consider in our sample, depending on their level of rarity (Jost, 2006). The results obtained from Simpson's and Shannon's indexes are shown graphically using scatter diagrams, where the values of Simpson's reciprocity index (1/D) and Shannon's homogeneity index (Evenness) are presented on the ordinate axis and the natural and Napierian logarithms of the MNI of each of the levels on the abscissa axis (Grayson and Delpech, 2002; Portero et al., 2022). In addition, the relationship between the indexes and the NISP of the studied levels was tested with Spearman's rank correlation coefficient between these variables, allowing us to observe the trend and strength of the relationship between both variables, as well as their statistical significance (*p*-value < 0.05).

2.3. Prey acquisition and transport

The search in the archaeological record for information about the processes of prey acquisition and transport requires the examination of skeletal profiles of taxa and size categories documented at sites in order to determine the introduction of animal carcasses by human groups. In this sense, ethnographic studies have sought explanations for transport decisions. Thus, depending on the size of the animal, the time of day, and the season when hunting takes place, the number of available porters, the distance to the base camp and the technology employed in their capture, animals will either be transported whole or certain anatomical parts will be selected for consumption at habitat sites (e.g., Lee, 1972; Binford, 1978; Bartram, 1993; Stiner, 1993; Monahan, 1998; Hawkes, 2001; Lupo, 2006).

In the taxonomic analysis, the higher or lower abundance of certain taxa can be used to explain hunting preferences for one or several of them (see, e.g., Altuna, 1972, 1995; Yravedra, 2002a, 2002b; Portero et al., 2019). To assess the taxonomic and anatomical representation of the macromammals present in the different study levels, we have used the Number of Remains (NR) and Number of Identified Specimens (NISP) data provided by the researchers in the literature of each of the contexts dated during the lower Magdalenian to evaluate the proportional weight of each taxon in them.

Once the taxonomic abundance was established, the anatomical representation was analysed in search of indicators of prey transport activity. To do this, the bone remains were grouped into skeletal parts by anatomical region, differentiating between cranial elements (antler, skull, maxilla, and mandible), axial elements (vertebra, rib, sternum, scapula, pelvis, sacrum and flat bone), forelimb elements (humerus, radius, ulna, carpal and metacarpal) and hindlimb elements (femur, patella, tibia, fibula, tarsals and metatarsal). When we were unable to ascertain whether they belonged to one or other appendicular region, the remains were included in the generic category of limb (metapodial, phalanx, sesamoid, and diaphysis and epiphysis of long bone) (Yravedra, 2006). Regarding the type of transport, it is to be expected that the nutritionally richest anatomical parts would be the ones most carried to the cave for consumption, which is known as the schlepp effect (Perkins and Daly, 1968). However, in many cases, the best represented parts are not the ones most frequently transported and consumed, as the destruction processes generated by biological and natural agents come into play (Yravedra, 2000, 2006).

2.4. Age patterns

To establish the type of hunting carried out by the human groups at the different sites, data on the age of the prey provided by different researchers have been used. For the study of age ranges, the mortality profiles of the macromammals in each of the levels were compared based on their classification into age categories (immature, juvenile, adult and senescent) (Stiner, 1990; Steele, 2002; Steele and Weaver, 2002). Given that faunal remains may be due to accumulation by humans and carnivores, for this research we have only considered individuals of those species for which researchers have been able to demonstrate their anthropogenic contribution to the site.

The results have been shown through bar graphs that include the percentages of infantile, juvenile, adult, and senile individuals for each species at each level. For greater precision in determining hunting strategy, we grouped the mortality profiles based on ternary graphs (Stiner, 1990), taking into account the four zonations established for each animal represented by Discamps and Costamagno (2015) and adapted to the life cycle of each species:

- "JPO" (Juvenile-Prime-Old) zone: includes sites with the following ratio: juvenile > adult > senile. Mainly refers to L-shaped mortality profiles (but also to a small U-shaped group).
- "JOP" (Juvenile-Old-Prime) zone: determined by the following class ratio: juveniles > senile > adults. Characteristic of the attritional profiles ("U" shape).
- Zone "P" (Prime): dominated by adult individuals.
- Zone "O" (Old): includes age profiles showing a mortality pattern with a predominance of senile animals.

2.5. Seasonality and catchment areas

From the age profiles described above and the biological reproductive cycles of present-day wild species, we can establish the seasonality of the occupations of a site by taking into account the periods of mating, gestation, birth, development and estimated life expectancy of animals (e.g., Costamagno, 1999; Discamps and Costamagno, 2015). For this research we considered biological studies on red deer (Clutton-Brock and Iason, 1986; Carranza, 2017), Iberian ibex (Alados and Escós, 2017), roe deer (Mateos-Quesada, 2017), horse (Outram and Rowley-Conwy, 1998; Waring, 2003), chamois (Pérez-Barbería, 2017), bison (Krasińska and Krasiński, 1995) and rabbit (Gálvez, 2017).

In order to establish the potential catchment areas for hunting resources, we have combined seasonal occupation data based on the age at death of prey with data on the seasonal migrations of these animals, based on a Digital Elevation Model of the Cantabrian Spain. For this we have used the MTN200 provincial maps by the National Geographic Institute (IGN), combined with bathymetric data provided by Bathymetric Compilation Group (GEBCO, 2020), treated with the free software QGIS v. 3.22 (QGIS Org., 2023). This has allowed us to visualize possible resource catchment areas depending on migratory movements in altitude, even in areas that are currently submerged under the sea. On these catchment maps we have included the seasonal occupation of the sites mentioned above, determining when they were active throughout the year, provided that the researchers have included this type of information in their publications. With all these data we have determined the estimated distance between these sites and the hunting resources depending on the time of the year.

2.6. Diet and energy intake

In order to establish the nutritional contribution of each of these species in the diets of the groups that inhabited the Cantabrian region between ca. 20-17 ky cal. BP, we have calculated the calories provided for each taxon consumed in the different sites. The following procedure was used (Portero et al., 2019, 2022):

- The mean weight of each taxon was established from the proportion of males and females of each species, based on current animal populations (Clutton-Brock and Iason, 1986). We used the mean weights for males and females of red deer (Carranza, 2017), Iberian ibex (Alados and Escós, 2017), roe deer (Mateos-Quesada, 2017), chamois (Pérez-Barbería et al., 2017), bison (Krasińska and Krasiński, 1995, 2002), horse (Waring, 2003), and rabbit (Gálvez, 2017).

- Calculation of the weight of meat[1] plus fat for each animal, based on the observations of Binford (1978) for caribou and sheep, applicable in the Cantabrian region to cervids and small bovids. For wild boar, we have taken the data from the nutritional tables of the Food Data Central Database of the US Department of Agriculture (USDA, 2020), and for the rabbit from the Spanish Food Composition Database (BEDCA, 2007). In addition, as the contribution of mammals' meat and fat varies significantly depending on the age of the individual, we have established a reduction in the weight of the adult animal of 33 % for juveniles and 66 % for immature individuals, broadly coinciding with the weights established in their life cycles (Portero, 2022; Portero et al., 2022). In this way, we have obtained the weight of the exploitable part of each of the animals.

- The calories per kilo of meat and fat for each of these animals were calculated with the data in the food tables of the US Department of Agriculture (USDA, 2020) and the Spanish Food Composition Database (BEDCA, 2007). These figures have allowed us to document the total energy provided by each specimen when multiplied by the weight contributed by its meat and fat (Table 1). To ensure that the contribution of the mammals documented in these sites is due to human activity, we only use those species that show signs of anthropic manipulation indicating that they were contributed and consumed by human groups.

This implies that some ungulates, such as reindeer, although present at some of the sites, have not been included as there is no evidence of their consumption. Also excluded are some marine mammals (Lefebvre et al., 2023).

All this, combined with the ecological and geographical parameters mentioned above, has allowed us to establish which prey contributed the most energy to the diet. To check whether the caloric representation could be underestimating small species since, being lighter in weight, they would tend to contribute less energy, Spearman's correlation coefficient was calculated between the percentage of total calories contributed by each taxon and the logarithm of MNI of these taxa. Thus, if we obtained a direct and statistically significant correlation between the two, we could assume that there is a relationship between the representation of these individuals and the calories provided; whereas, if we obtained an inverse and non-significant correlation, we would find no correspondence for these variables.

This energy contribution has allowed us to classify the levels based on their energy intake and to determine how many days they could have fed a hypothetical group of 10 adults with an energy expenditure of about 2263 kcal/day, as established by ethnographic studies (Pontzer et al., 2012).

2.7. Profit from prey

To establish the economic profitability that each of these species provided in the different deposits in the Cantabrian region, we have taken into account the search time, handling time and return rates, aspects that affect the costs of obtaining the prey and that, in combination with the energy provided, allows them to be positioned in a ranking of prey (MacArthur and Pianka, 1966; Simms, 1987; Henrikson, 2004;

Marín, 2010; Stiner et al., 2008; Portero et al., 2019).

Regarding the search time for a species, two fundamental factors intervene: population density and encounter ratio. We have estimated population densities in the Cantabrian region based on information on current animal populations. Thus, the population density of red deer (8.05 ind/km^2), Iberian ibex (11.11 ind/km^2), roe deer (16.61 ind/km^2) and chamois (15.82 ind/km^2) (Marín, 2010) is based on the allometric relationship of Nowak (1999). For large bovids we have applied the average of the population peaks observed between summer and winter in Prince Albert National Park in Canada (Merkle et al., 2015), which is 1.8 ind/km^2. For horse, we have reference data from ranges in the New Forest (England), where population density varies between 0.8 and 10.2 ind/km^2 (Tayler, 1972). From these estimates, we have established an average of about 5.5 ind/km^2 for northern Spain. For rabbit, the peninsular data establishes an average of 5 ind/ha (Gálvez, 2017); however, this figure is much higher than the real number in the Palaeolithic in the Cantabrian region, since it is a species whose population density is greatly affected by the climate and the availability of habitat. For this reason, we have decided not to include it in the profitability calculations, given its limited contribution to the region's deposits. Once the population density was established for these species, we were able to assess the encounter rate in relation to this population density.

Regarding the handling time of prey, for red deer and Iberian ibex, it is estimated to be about 2 h, for roe deer and chamois one and a half hours, and nine for bison (Marín, 2010). For horse, we have applied 9 h of manipulation (Portero et al., 2019). In the case of rabbit, we have used the processing time proposed by Simms (1987) for *Lepus townsendii* in the Great Basin, which coincides with what was observed for this species by Henrikson (2004) on the Snake River Plain in Idaho, which sets a handling time at 0.075 h (4.5 min).

With the data on the energy contribution of each species and their handling rates, we have calculated the energy benefit of these species depending on their processing time and energy contribution, obtaining the calories that each of them can supply per hour (Simms, 1987; Henrikson, 2004). All of this allows us to establish a ranking of the main prey documented in the Cantabrian region during the lower Magdalenian based on energy benefit (Table 2).

3. Results

Of the 19 selected sites, 11 are located in coastal valleys (El Cierro, Cova Rosa, Tito Bustillo, La Riera, El Linar, Las Aguas, Cualventi, Altamira, El Juyo, Santimamiñe and Ekain), four are mountain sites (Los Canes, Coímbre B, El Rascaño and Erralla) and four would be found in areas of interior valleys (Las Caldas, Arangas, La Güelga and El Mirón). For the studied sites, we have data from the following levels: in Asturias, Cierro F, G and G1 (Álvarez-Fernández et al., 2016; Portero et al., 2019), Cova Rosa B6 (Álvarez-Fernández et al., 2019, 2021), Tito Bustillo 1 and 2 (Altuna, 1976; Álvarez-Fernández et al., 2015; Moure, 1997), Caldas XIII, XII, XIIi and XI (Altuna and Mariezkurrena, 2017; Corchón, 2017), Riera 19 (Altuna, 1986; Straus, 1986), Canes 2B (Arias, 2002, 2013), Arangas F and G (Álvarez-Fernández et al., 2020), Güelga 3 (Menéndez et al., 2005; Rojo, 2020) and Coímbre B4 (Álvarez-Alonso and Jordá Pardo, 2017; Yravedra et al., 2017); in Cantabria, Linar 3C, Aguas B, Cualventi E (Castaños, 2016; Rasines del Río, 2016), Mirón 115 and 504 (Carvalho et al., 2021; Hopkins et al., 2021; Marín and Geiling, 2015), Juyo 4 and 7 (González-Echegaray, 1987; Klein and Cruz-Uribe, 1987), Rascaño 3, 4 and 5 (Altuna, 1981; Barandiarán and González-Echegaray, 1981) and Altamira 2 (Castaños and Castaños, 2014; González-Echegaray, 1988; Rasines del Río, 2016); in the Basque Country, Santimamiñe Csn-Camr (Castaños and Castaños, 2011; López-Quintana and Guenga, 2011), Ekain VII (Altuna, 2012; Altuna and Mariezkurrena, 1984) and Erralla V (Altuna, 1985; Altuna and Mariezkurrena, 1985).

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[1] In this paper we use "meat" to refer only to flesh material of animal origin and "meat resources" to refer to animal resources *sensu lato* (i.e., animal foods, including muscle, fat, and offal) (Speth, 2024).

Table 1

Caloric energy provided by taxon and age category of the main species documented in the Cantabrian region during the Upper Pleistocene and Holocene, based on the average weight of both sexes (sex ratio) and the proportion of meat and fat provided by each individual by age category (AD = adult; JU = juvenile; IMM = immature).

Species	Age Cat.	Average weight (kg)	Meat + fat (kg)	Energy (Kcal/kg)	Total Energy (Kcal)	References
Cervus elaphus	AD	93.5	36.7	1,110	40,737	Clutton-Brock and Iason (1986); Marín (2010); Carranza (2017);
	JU	62.4	24.5	1,110	27,195	USDA, 2020
	IMM	31.1	12.2	1,110	13,542	
Capra pyrenaica	AD	51.2	19.4	1,140	22,116	Marín (2010); Alados and Escós (2017); USDA, 2020
	JU	34.2	13	1,140	14,820	
	IMM	17	6.4	1,140	7,296	
Rupicapra pyrenaica	AD	26.5	10	1,140	11,400	Marín (2010); Pérez-Barbería et al. (2017); USDA, 2020
	JU	17.7	6.7	1,140	7,638	
	IMM	8.9	3.3	1,140	3,762	
Capreolus capreolus	AD	24.4	9.5	1,110	10,545	Marín (2010); Mateos-Quesada (2017)
	JU	16.3	6.3	1,110	6,993	
	IMM	8.1	3.2	1,110	3,552	
Bos/Bison	AD	600	300	1,220	366,000	Krasińska and Krasiński, 2002;
	JU	399.6	200	1,220	244,000	Marín (2008)
	IMM	200	100	1,220	122,000	
Equus ferus	AD	210.25	147.1	1,080	158,868	Outram and Rowley-Conwy (1998); USDA, 2020
	JU	140.2	97.5	1,080	105,300	
	IMM	70.1	49	1,080	52,920	
Oryctolagus cuniculus	AD	1.3	0.34	1,320	448.8	BEDCA, 2007; Gálvez (2017)
	JU	0.87	0.23	1,320	303.6	
	IMM	0.43	0.11	1,320	145.2	

Table 2

Ranking of the main species consumed in the Cantabrian region based on the energy benefit they report per hour. The model integrates the total meat and fat, the energy per kg of that meat and fat, and the processing time of those resources.

Species	Meat + fat (kg)	Energy (Kcal/kg)	Processing time for 1 kg of meat (h/kg)	Processing time of the prey in hours (kg x h/kg)	Energy supply (Kcal/h)	Ranking
Bos/Bison	300	1,220	0.03	9	40,666.7	1
Cervus elaphus	36.7	1,110	0.054	2	20,368.5	2
Equus ferus	147.1	1,080	0.061	9	17,652	3
Capra pyrenaica	19.4	1,140	0.103	2	11,058	4
Rupicapra pyrenaica	10	1,140	0.15	1.5	7,600	5
Capreolus capreolus	9.5	1,110	0.158	1.5	7,030	6
Oryctolagus cuniculus	0.34	1,320	0.206	0.075	5,984	7

3.1. Palaeoecological analysis

The result of the ecological diversity analysis of the 32 Magdalenian levels can be seen in Appendix 1, Table 2. During the lower Magdalenian, the correlation between the NISP and the homogeneity data (Evenness) from the Shannon index indicates an inverse relationship, moderate and statistically significant, between these variables. This indicates that there is a linear relationship between homogeneity and NISP ($\rho = -0.61$; $p=<0.001$) (Fig. 2). The higher the NISP, the more heterogeneous the sample. Arangas F and Arangas G are the most homogeneous levels, while Erralla V, Cualventi E, Altamira 2 and Juyo 4 would be the ones that present the least uniformity. The Effective Number of Species stands at an average of 2.01 ± 0.11, which indicates a low taxonomic richness at this time, with values ranging between 1.3 and 3.6. From Simpson's reciprocal index ($1/D$), we find that the frequency of one taxon is high in all levels. In this case, the correlation between NISP and Simpson's reciprocal index is not statistically significant, so there is no linear relationship between these two variables (Fig. 3).

According to the scatter plot, Altamira 2, Cualventi E and Aguas B are the ones with the greatest abundance of one taxon and the least diverse. Although the high frequence of one taxon is pronounced in this period, we find levels that do not present a clear abundance of a single taxon in the %NISP, more specifically in the levels Arangas F, Arangas G, Mirón 115, Caldas XI and XII (see, Fig. 3). Quesada (1997) proposed that diversified hunting behaviour could begin to be seen from 2.45 on

Simpson's reciprocal index. However, according to this premise, none of the levels analysed exceed the proposed figure.

The taxonomic representation indicates that red deer is the most frequent taxon in 20 out of 32 levels, exceeding 60% of the NISP (Appendix 1, Fig. 1). Furthermore, in 10 of these levels, the figure is above 90%. Iberian ibex is the most abundant species in 10 of them, exceeding 60% of the NISP. Only in Arangas F and Mirón 115 is this figure lower, about 45%. Horse is the main species in Caldas XI and XII, but in no case does it exceed 50%, sharing importance with red deer. It is worth noting how the oldest levels at Las Caldas (Levels XIII and XIIi) are dominated by red deer, while in the two most recent levels (Levels XII and XI) horse occupies the first place in the assemblage (Altuna and Mariezkurrena, 2017). Chamois only appears in significant percentages in Los Canes, La Güelga and Arangas, but in no case does it exceed 13% representation. In the case of Arangas G, roe deer seems to be relatively important (17.9% of NISP), while in the rest of the sites it appears in percentages <5%. Large bovids are present in almost all the levels, but their frequency in no case exceeds 5%.

3.2. Acquisition and transportation of prey

The anatomical representation patterns of red deer show that all the anatomical elements of the animal are present in the sites, except in Rascaño 3, where no axial elements are documented (Appendix 1, Fig. 2). Cranial elements are well represented in all levels, being very abundant in Güelga 3, while Arangas F records the lowest
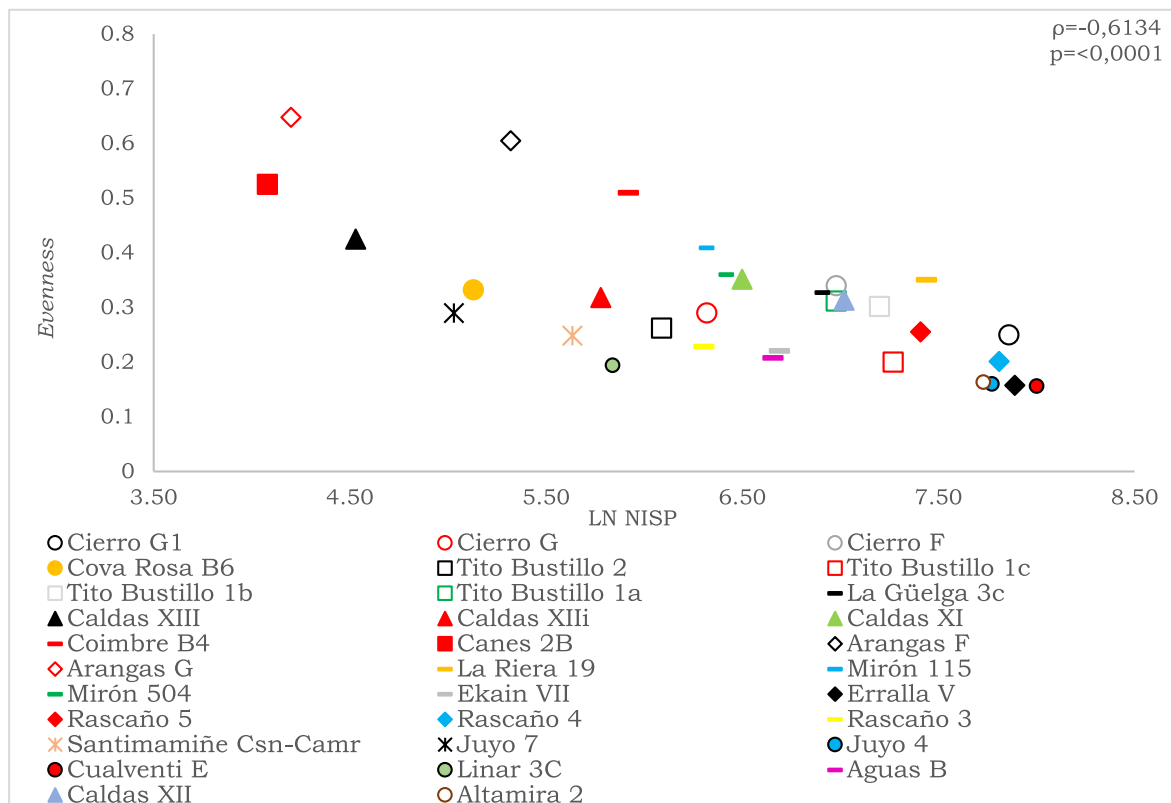
Fig. 2. Graph showing the relationship (Spearman rs) between the taxonomic representation (LN. NISP) and the Shannon homogeneity values (Evenness) in the different Magdalenian levels in the Cantabrian Spain.
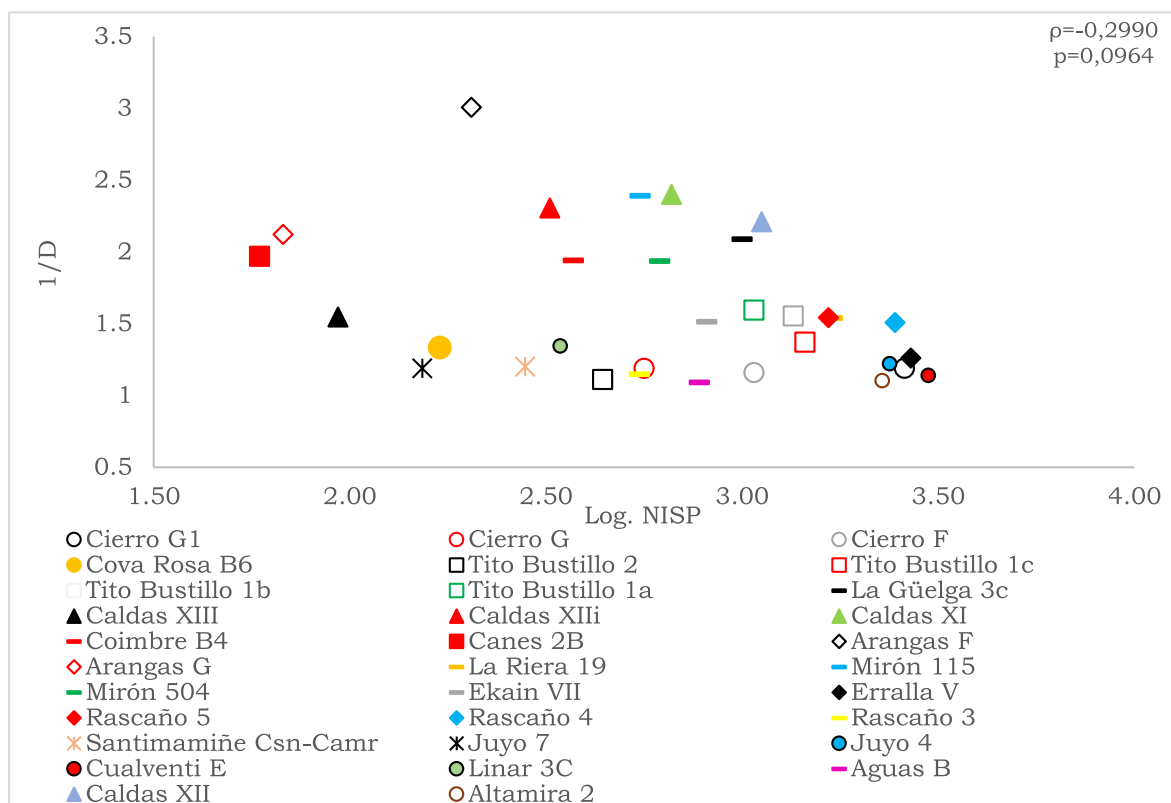

Fig. 3. Graph showing the relationship (Spearman rs) between the taxonomic representation (Log. NISP) and Simpson's reciprocal index (1/D) in the different lower Magdalenian levels in the Cantabrian Spain.

representation, this being precisely one of the sites in which this animal was not the main species captured. Axial elements are the least abundant, but they become the majority in Ekain VII and in Caldas XIIi, although in general they are at values <20%. The relative abundance of these elements could indicate that red deer were transported completely to the site in all these levels at some point. Nevertheless, we cannot rule out that the lower percentage of appendicular elements in these sites is due to their being more fragmented due to the fracturing process to extract the marrow. However, axial parts were more frequently abandoned in Arangas F, Rascaño 5, Rascaño 4 and Rascaño 3. The limbs are also widely represented in all levels. Most of them correspond to phalanges and metapodia, which are best represented in Santimamiñe Csn-Camr.

Iberian ibex appear with an abundant number of axial elements in almost all the levels, except for Cierro F. Hindlimb elements also appear in a large percentage, exceeding 40% in Arangas F, Arangas G and Cierro F. Cranial elements present discrepancies between those sites with a large percentage, such as Cierro G1, Cierro G and Erralla V, and those that show little representation, such as Santimamiñe Csn-Camr, Arangas F and Caldas XIIi. This seems to indicate that there was a different transport strategy in these levels but, in any case, their distribution tells us that the animals could have been transported completely at some point in all of them (see Appendix 1, Fig. 2). Regarding chamois, except in Arangas F and Canes 2B, its importance is very slight and does not allow comparisons about its anatomical representation.

Among large mammals, only horse shows sufficient elements for comparison in Caldas XII, Caldas XIIi, and Tito Bustillo 1 (see Appendix 1, Fig. 2). Cranial elements are very abundant, due to the good preservation of the animal's teeth, while axial elements are the least numerous. As for the limbs, hindlimbs are more abundant in Caldas XII and XIIi, while forelimbs are more abundant in Tito Bustillo 1a and 1c. In any case, the abundance of these elements could indicate a more frequent transport of these anatomical parts in both caves.

3.3. Age patterns

The age of death of ungulates documented in the lower Magdalenian levels shows a greater number of captures of adult animals than of immature, juvenile and senile animals (see Appendix 1, Figs. 3–7).

If we qualify by species, red deer presents an abundant percentage of adult individuals, and in some levels such as Coímbre B4 they even represent 100%. However, immature and juvenile individuals are also widely represented in most of the caves, and they constitute the majority in Ekain VII and Erralla V. In the latter, immatures constitute the total number of documented red deer. Senile individuals are the least represented, but they maintain a good proportion in Caldas XII and XIIi, where they exceed 20%. In any case, most levels show a balance in the age categories of the hunted prey. The graphic representation in the ternary diagrams shows that most of the red deer captures occur in the "JPO" zone, with a small number of them in the "P" zone (Appendix 1, Fig. 3).

In the case of Iberian ibex, a greater number of adult individuals are documented in almost all levels (Appendix 1, Fig. 4). Only in El Mirón 504 are juveniles more abundant than mature animals. There is also a considerable number of caves that present a balance between adults and immatures, such as Arangas G and F, Caldas XI, Caldas XIIi, Tito Bustillo 2 and Cierro G. Senescent individuals are only present in Caldas XI and XII, where their proportions are significant (25% and 33% respectively). The situation of this species in the ternary graph indicates how, in this case, a large part of the catches belongs to a "P" profile, where adults are the majority.

Chamois has a minor importance, with Güelga 3 being the one site that has contributed the highest MNI of this species (MNI = 7) (Appendix 1, Fig. 5). In this species, we find a predominance of adults over juveniles, reaching values between 50% and 100% representativeness. Immature individuals are only documented in Coímbre B4, while senile

ones are absent. Juveniles share the same percentage as adults in Arangas F, Ekain VII and Caldas XI. Although the data are scarce, their distribution in the ternary diagrams indicates how the majority of captures fall in the "P" and "JPO" zone, in accordance with the predominance indicated for these animals.

Among the large prey, horse appears with a large percentage of adults in almost all levels, reaching 100% in Tito Bustillo 2. In some cases, such as in Güelga 3, Caldas XI and Caldas XIII, they share importance with juveniles, but in general the latter are less abundant. For this species, no immature individuals have been documented and senile ones are only found in Caldas XI, XII, XIIi and XIII, with percentages between 30% and 50% representativeness. The representation of this species in the ternary graphs shows that a small group of sites maintain a "JPO" strategy, while the levels in Las Caldas fall into the "P" and "O" zone, highlighting a majority consumption of adults (Appendix 1, Fig. 6).

Regarding large bovids, we have data from eight levels for comparative analysis, all of them based on two or three individuals. For this taxon, a large number of adults have been documented; up to 100% of the catches in Coímbre B4, Ekain VII and Tito Bustillo 1a. In Caldas XII, Tito Bustillo 2 and Tito Bustillo 1c there is a balance between adults and juveniles, and one immature individual was documented in Cierro G1. The ternary graphs for this species show a dispersion of catches over the "P" and "JPO" zones (Appendix 1, Fig. 7).

The rest of the documented species do not count with enough individuals to establish a comparison, although they are a resource that we will consider in the analysis of the seasonality and energy contribution of these animals to the diet.

3.4. Seasonality and catchment areas

From the mortality patterns it can be observed that most captures were made during spring and summer, as can be seen in Ekain VII (Altuna and Mariezkurrena, 1984), Caldas XIII and XI (Altuna and Mariezkurrena, 2017), Tito Bustillo 1a and 1b (Altuna, 1976), Rascaño 3 (Altuna, 1981) and Aguas B (Castaños, 2016). However, we also have levels that were occupied during autumn and winter, such as Mirón 504 (Marín and Geiling, 2015), Güelga 3 (Rojo, 2020), Tito Bustillo 1c (Altuna, 1976) and Rascaño 5 (Altuna, 1981). There is also a small group in which captures could be carried out throughout the year, due to the wide spectrum of documented individuals. This is the case of Cierro G1 (Portero, 2022), Rascaño 4 (Altuna, 1981), Cualventi E and Linar 3C (Castaños, 2016). It is precisely in these levels that the highest MNI of all those analysed have been recorded. However, seasonal occupancy in many of these levels is associated with two or three individuals captured at a given time and there is therefore a wide margin of possibility. Therefore, these data should be considered only as approximations to the occupation of a cave throughout the year.

From the Digital Elevation Model, we can visualize the potential catchment areas of the main hunting resources based on their seasonal movements and the previously mentioned occupation of each of the caves. Data on the seasonality of the catches, the height location of these caves and their distance from the coastline are shown in Table 3.

The map shows that, during spring, when red deer are migrating to areas above 500 m above sea level and Iberian ibex and chamois are at the highest altitudes in their seasonal movement, Cierro G1, Cierro G, Cierro F, Cualventi E, Linar 3c, Rascaño 5, Rascaño 4, Riera 19, Aguas B, Mirón 115 and Mirón 504 were all occupied. In all levels red deer could be transported from areas of about 2 km around the sites. Regarding the hunting of crag animals, given that during the spring they are found at a higher altitude, we only have evidence in sites where access to these resources is relatively close, such as in Mirón 504, Rascaño 5 and Rascaño 4. Large bovids, given their short seasonal movements, would be found between 400 and 1000 masl and therefore could be captured in a range of 7 km from all the caves where they are represented (Fig. 4).

The most intense occupation of the territory was during summer.

Table 3

Location, altitude, and distance to the current coastlines (DCA) and during the lower Magdalenian (DCMI) from marine regression data (Thompson and Goldstein, 2006; Jordá Pardo et al., 2018), and seasonality estimated during the lower Magdalenian from ungulate hunting. SP = spring; SU = summer; A = autumn; W = winter; ND = no data.

Site	Region	Altitude	DCA (km)	DCMI (km)	Seasonality
Altamira	Cantabria	160	4	9.5	ND
Arangas	Asturias	340	10	17	ND
El Cierro	Asturias	82	2	6	SP-SU-A-W
Coímbre B	Asturias	135	10	14.5	A
Cova Rosa	Asturias	170	4	8	ND
Cualventi	Cantabria	65	2,5	9.5	SP-SU-A-W
Ekain	Basque Country	90	7	12.5	SU-A
El Juyo	Cantabria	92	4.5	11	ND
El Linar	Cantabria	104	6	13	SP-SU-A-W
El Rascaño	Cantabria	275	20	27	SP-SU-A-W
Erralla	Basque Country	230	10	14.5	SU-A-W
La Güelga	Asturias	180	15	20.5	A-W
La Riera	Asturias	30	1.5	7	SP-SU-W
Las Aguas	Cantabria	40	2.5	9.5	SP-SU-W
Las Caldas	Asturias	160	30	36.5	SP-SU-W
Los Canes	Asturias	325	11	18	ND
El Mirón	Cantabria	260	20	29.5	SP-SU-A-W
Santimamiñe	Basque Country	137	6	11	ND
Tito Bustillo	Asturias	200	0.5	5	SU-A-W

Except for Tito Bustillo 2, Mirón 504 and Coímbre B4, the rest of the levels were occupied at this time. In this season red deer are found at altitudes above 500 masl, when females nurse their newborn fawns. It is precisely at this time that hunting for this ungulate intensifies in caves such as Ekain VII, Cualventi E and Cierro G1. In this season the catchment area in the sites located in the valleys is further away than during spring, with its range being around 5 km, so transportation would be harder. Regarding crag animals, they continue at high altitudes, although now they are hunted more frequently than in spring, as some captures in Rascaño 4, Rascaño 5 and Mirón 504 seem to indicate, focusing mainly on adult and juvenile animals. In these caves red deer were also hunted at this time, which fits with the higher altitude of their migration during summer, when they would be found in areas near those caves. The few captures of large bovids could have occurred in about 3 km around Las Caldas, El Cierro, Tito Bustillo, Ekain and Coímbre B in this season.

During autumn the number of red deer captures decreases, as does the occupation of many of the caves used in summer. At this time they appear in Tito Bustillo, La Güelga, Coímbre B and Rascaño. In this season, red deer move to lower zones because of the rut, becoming a hunting target within a 2 km perimeter around the caves. Crag animals begin their migration to lower altitudes and are thus represented in the levels where this type of taxa is more abundant (Coímbre B4, Güelga 3 and Rascaño 4). It seems logical to think that in the autumn the capture of these animals in areas close to the cave could have been easier, especially considering that it is the mating season and chamois usually occupy open spaces (Pérez-Barbería, 2017). The large bovids were able to descend to somewhat lower heights than in the previous season and would be found in areas about 2 km from all the caves with the presence of this mammal.

In winter, the occupation of sites with high percentages of red deer NISP is the least intense of all periods. Furthermore, this coincides with the time when red deer are at the lowest altitudes in their seasonal movement and could be more accessible in sites in coastal valleys. Perhaps the captures of adults from levels that show long occupations such as Cualventi E, Linar 3c and Cierro G1 took place there. Furthermore, it is the season in which a large number of rocky animals were hunted in La Güelga, Coímbre B, El Mirón or El Rascaño, coinciding with

the rise of this species again to high mountain areas and, therefore, furthest from said caves (approx. 5 km). Finally, if large bovids had been hunted at this time of year, they would have been captured at the lowest altitudes close to the coast.

The results presented are only those that can be analysed from the captures of macromammals and, therefore, are limited to the identification of the species and the chronological markers of the moment of slaughter. We are also aware that the migration system may vary depending on the geographical area, climate, and the animals' ability to adapt. Thus, the proposed approaches to seasonal hunting should always be taken with caution given the limitations they present.

3.5. Diet and energy intake

We have calculated the calories which each of these taxa contributed to the diet of human groups in the Cantabrian region during the lower Magdalenian. Given the absence of taphonomic information on anthropogenic alterations or on the age of the individuals at death, for some levels it has been impossible to quantify the anthropic contribution; thus, the levels Rascaño 5 to 3, Altamira 2 and Tito Bustillo 1 and 2 have been excluded. In Cualventi E, Linar 3c and Aguas B we only have the ages and evidence of consumption for red deer, so only this species will be included in the energy calculation. The case of Erralla V is similar since, although we have the age of the red deer and Iberian ibex, we do not know the age of chamois to be able to calculate its energy contribution. Therefore, we have not been able to quantify this prey, which displays traces of anthropic manipulation. In the case of Santimamiñe Csn-Camr we have only been able to count the energy contribution of adult red deer, since they are the only ones in the category of medium mammal, whereas immature red deer and the rest of the taxa have been excluded due to their inclusion in the taphonomic study within the categories of large and small mammals, without being able to specify the precise species to which each of the taphonomic alterations refers (San Pedro and Cáceres, 2011). Detailed information on the energy calculation of each taxon for each selected level is presented in Appendix 1, Table 3.

From the calculation of total calories contributed by taxa with evidence of anthropic manipulation, red deer is the animal that would have provided the greatest amount of food for the human groups, accounting for 52.8% of the total calories documented in the selected sites. Although anthropic manipulation of horses is only documented in seven levels, this taxon is in second place in terms of calories contributed, with around 19.8% of the total. Large bovids would be in third place, contributing 17%, followed by Iberian ibex with 8.8%. Roe deer and chamois, due to their low MNI, would have supplied very little energy to the total amount ($\leq 1\%$) (Fig. 5).

To corroborate whether there is a statistically significant relationship between the size of the prey and the total count of calories that each of them contributed during the lower Magdalenian in the Cantabrian Spain, we have calculated the Spearman correlation coefficient between the % of Kcal supplied by each taxon and the logarithm of the MNI of each of them. The result shows a direct and moderate but non-significant relationship between both variables, which means that there is no linear correlation between the energy contribution made by each taxon and the MNI of individuals of those species (Appendix 1, Fig. 8).

Taking into account the importance of each of these levels in the global energy representation, Cierro G1 is the one that could have supplied the greatest caloric energy to human groups during the lower Magdalenian, with just over 2.66 million Kcal and about 2,334 kg of meat and fat, while Arangas G would have been the one that would have reported the least energy with a total of 65 kg of meat and fat and around 80,865 kcal (0.5%) (Appendix 1, Fig. 9).

From the calculation of calories by species, red deer is the mammal energy source in the diet in 12 of the 20 levels for which its contribution has been calculated. Horse is the species that supplied the most in Caldas XIIi, Caldas XII and Caldas XI, while large bovids contributed the most in
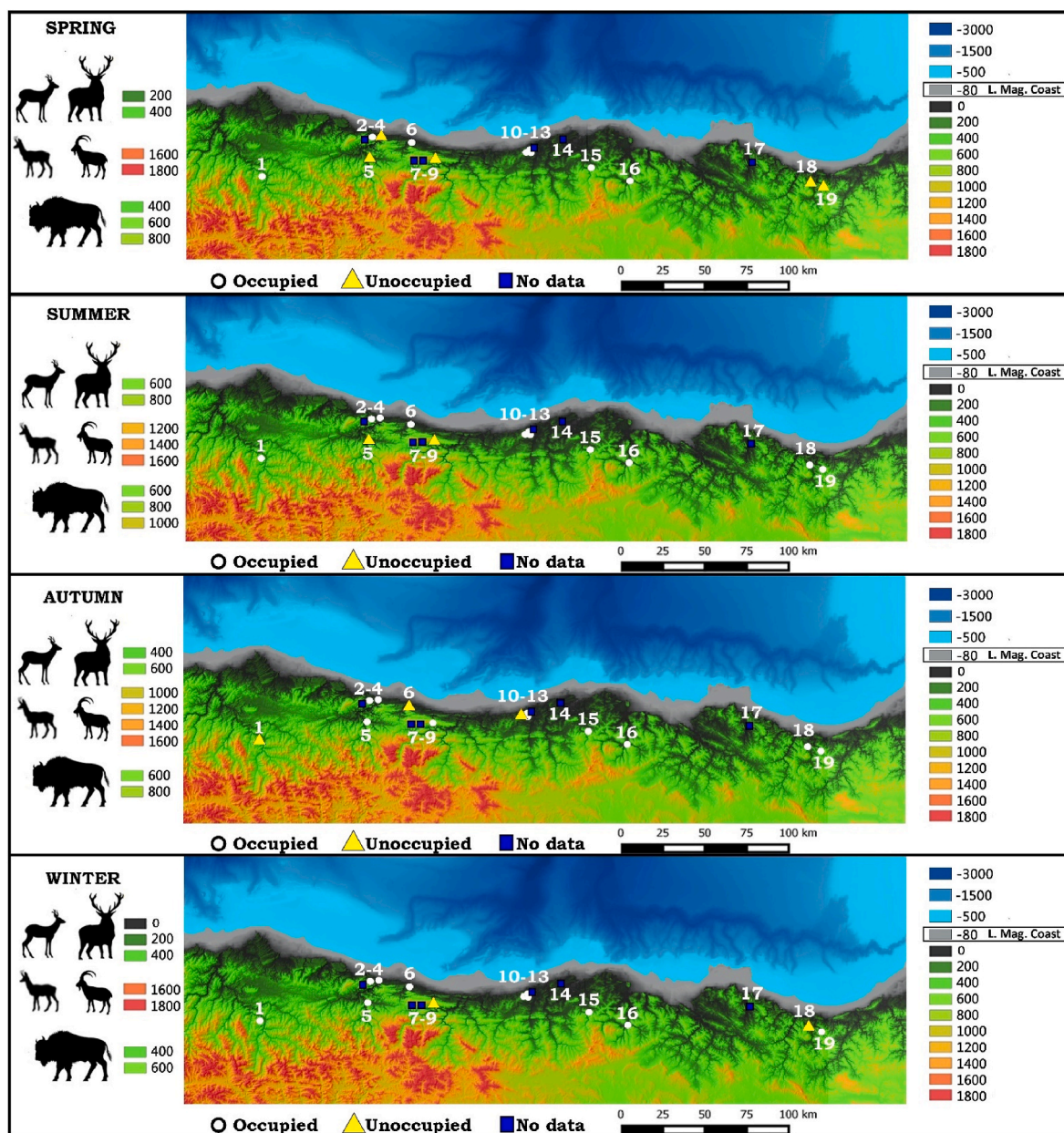
Fig. 4. Digital elevation model of the Cantabrian Spain with bathymetric data indicating the coastline during the lower Magdalenian modelled from QGIS v. 3.22 and the IGN and GEBCO maps. It includes the location at altitude of the species hunted during different times of the year and the seasonal location and occupation of the selected caves. 1) Las Caldas; 2) Cova Rosa; 3) El Cierro; 4) Tito Bustillo; 5) La Güelga; 6) La Riera; 7) Arangas; 8) Los Canes; 9) Coímbre B; 10) Las Aguas; 11) Cualventi; 12) El Linar; 13) Altamira; 14) El Juyo; 15) El Rascaño; 16) El Mirón; 17) Santimamiñe; 18) Ekain; 19) Erralla.
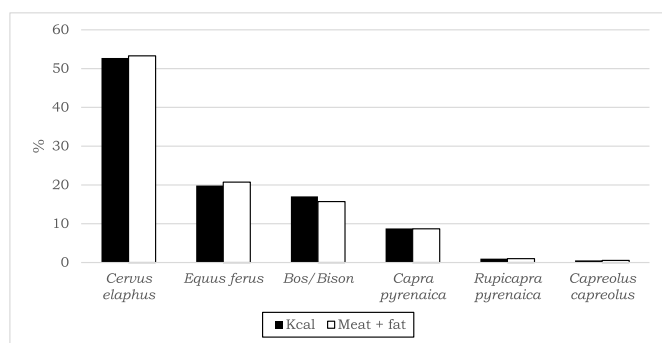

Fig. 5. Total percentage of calories and potential meat and fat (kg) contributed per taxa at lower Magdalenian sites in the Cantabrian region.

Caldas cave. Although Iberian ibex are present in most of the selected levels, only in Arangas G and Erralla V were they the main energy contribution. Chamois and roe deer are very rare and do not exceed 12% of the energy contribution in these levels. The former is relatively important in Güelga 3, while the latter's supply is most significant in Arangas G (Fig. 6).

From this caloric energy provided by the ungulates, we can estimate the time they were able to feed a group of 10 adults solely by consuming these resources. To do this, we used the average energy expenditure of 2263 kcal per person per day estimated for Hadza hunter-gatherer groups (Pontzer et al., 2012). The result indicates that in Cierro G1, these resources were able to feed a group of about 10 adults for more than 117 days, while, in Arangas G and Aguas B, they were barely able to do so for just over a couple of days (Appendix 1, Fig. 10).

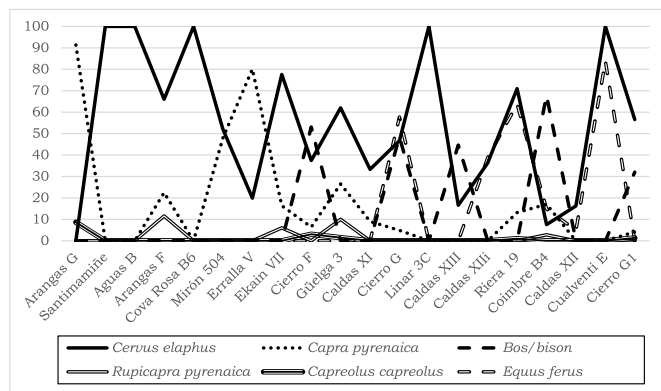Despite these approximations, it should be noted that the formation

Fig. 6. Percentage of calories provided by each taxon in different lower Magdalenian levels.

process of these faunal assemblages could have involved prolonged events over time and that the excavated volume has not been the same in each of the archaeological levels of these caves.

Regarding the profitability of each species, we have taken into account the handling time, the proximity of their catchment areas, the population density and the energetic benefit that each taxon could contribute. At first glance it might seem that smaller prey would be more profitable due to the lower cost of transportation and handling and their higher population density. However, the distance to their catchment areas and their lower caloric intake plays an important role in their energy efficiency. In this way, the ranking of prey with which we started for the Cantabrian region has been modified based on the data obtained (Table 4).

4. Discussion

The results obtained from the palaeoecological and palaeoeconomic analysis of the 32 levels of study have allowed us to understand subsistence strategies in the Cantabrian region between ca. 20,000 and 17,000 cal. BP.

From the taxonomic studies we see that the predominance of red deer is clear in lower Magdalenian levels (62.5% of the sites). However, Iberian ibex was also an important prey, especially in places like El Rascaño, where it exceeds 90% representation in some levels. Therefore, it is evident that only two species display NISP values that may indicate specialization: red deer and Iberian ibex. These results are quite consistent with the outcome of palaeoecological analyses, where the low diversity of species showed a pattern clearly dominated by a single taxon. These data on hunting specialization have already been widely commented on by different specialists, who agree that during the lower Magdalenian specialization on these two taxa became generalized depending on the location of the sites (e.g., Altuna, 1979, 1990, 1995; González Sainz, 1992; Quesada, 1997; Yravedra, 2002a). However, at this time a few deposits diversified with a spectrum of taxa, such as

Arangas F, Mirón 115, Caldas XI and Caldas XII, which was explained by their proximity to different biotopes (Portero et al., 2019). These data have a close relationship with the neighbouring region of southern France during the Magdalenian, where the reindeer acquired the importance that the red deer had in the Cantabrian region, being a predominant prey in sites in the Perigord, Quercy and the Paris Basin (Costamagno, 2001; Kuntz and Costamagno, 2011; Pétillon et al., 2016; Fontana, 2017). However, only in 42.5% of the sites do reindeer predominate with more than 80% of the NISP, something that also happens with the red deer in the Cantabrian region where 43.8% of the sites analysed exceed 80% of NISP.

Regarding transportation, the anatomical representation of red deer indicates that all parts of the animal are present in practically all the levels. This is something that is also observed for reindeer in the south of France (Kuntz and Costamagno, 2011). However, at sites where red deer is not the main prey (such as in La Güelga, Arangas and El Rascaño) the cranial and axial elements are very scarce, which could be indicating transport of the elements with greater use since red deer would have to be hauled from a greater distance. In interior valley sites, it seems that axial elements are abundant and even a majority in some of them. This pattern seems to indicate that red deer would have been carried whole more often at those locations. In contrast, Iberian ibex appears with an abundant number of axial elements in almost levels, so it must have been transported complete frequently. Regarding these two taxa, it should be noted that taphonomic alterations, in those sites with studies of that type, show that red deer was consumed in all of them, either through cut marks or fracturing to access the marrow (except in Arangas G), while Iberian ibex was only consumed in 13 of the 32 levels (Yravedra, 2002a; San Pedro and Cáceres, 2011; Castaños and Castaños, 2014; Marín and Geiling, 2015; Castaños, 2016; Altuna and Mariezkurrena, 2017; Yravedra et al., 2017; Portero et al., 2019; Álvarez-Fernández et al., 2019, 2020; Rojo, 2020; Carvalho et al., 2021; Portero, 2022).

Regarding large prey, the most abundant is horse. The skeletal profiles for this species point to greater transport of the animal's limbs, especially in those levels where horse is one of the main species, such as in Caldas XII and XIIi.

One of the most relevant aspects to establish the type of hunting strategy is the mortality profiles. Although these profiles are very different between levels, we can see that in most cases mortality indicates a hunting strategy focused on immature and young adult red deer. This strategy of capturing red deer and their fawns in spring and summer is documented for this period in Ekain VII (Altuna and Mariezkurrena, 1984), Erralla V (Altuna and Mariezkurrena, 1985), Riera 19 (Altuna, 1986), Linar 3C (Castaños, 2016), Tito Bustillo 1 and 2 (Altuna, 1976) and Cierro G1 (Portero, 2022). However, there are other sites that present a strategy focused on the capture of adults of both sexes, such as Güelga 3 (Rojo, 2020), Aguas B (Castaños, 2016) or Cualventi E (Castaños, 2016).

In the case of Iberian ibex, unlike the red deer, it could be indicating an individualized capture of adults in their reproductive stage, while juveniles and senile individuals were less hunted. However, in some sites with abundant Iberian ibex, such as El Rascaño (Altuna, 1981) and

Table 4
Summary of the energy contribution of macromammals during the lower Magdalenian in the Cantabrian region, with their processing time, population density, radius of catchment area and their position in relation to the energy ranking of prey.

Taxa	%Kcal provided	Meat weigh + fat (kg)	Handling time (hours)	Density (ind/km²)	Radius of catchment area (km)	Position in the ranking of the Cantabrian region
Cervus elaphus	52.8	7,453	2	8.05	0–5	2
Equus ferus	19.8	2,898	9	5.5	0–5	3
Bos/Bison	17	2,200	9	1.8	5–9	1
Capra pyrenaica	8.8	1,216	2	11.11	1–9	4
Rupicapra pyrenaica	1	140	1.5	15.82	1–9	5
Capreolus capreolus	0.5	76	1.5	16.61	0–5	6

Erralla (Altuna and Mariezkurrena, 1985), animals of all ages and both sexes were hunted, which indicates that there was a wide spectrum of captures in the mountain sites where this taxon is abundant.

In the case of large prey, such as horses and large bovids, representation based on ternary graphs has shown a clear predominance of adults, with captures belonging to zone "P" and zone "JPO". A preference for senile individuals ("O" Profile) has even been observed in Caldas XII and XIII. This indicates that large preys were consumed mostly in their adult stage and probably through individualized hunting.

The seasonality of the occupations has been established from the mortality profiles. In the Cantabrian Spain, more captures were made during spring and summer, as seen in Ekain VII, Caldas XIII, Caldas XI, Tito Bustillo 1a, Tito Bustillo 1b, Rascaño 3 or Aguas B. However, other levels reflect occupation during autumn and winter, such as Mirón 504, Güelga 3, Tito Bustillo 1c and Rascaño 5. There is also a small group in which captures could be carried out throughout the year, due to the wide spectrum of documented individuals; this is the case of Cierro G1, Cualventi E, Linar 3C and Rascaño 4. The highest MNI of all those analysed have been recorded precisely in those levels. Studies on mortality profiles have also been applied in the south of France, obtaining good results on seasonal occupation through the analysis of reindeer in La Dordogne (Fontana, 2017). Although for the Cantabrian Spain red deer are captured mostly in spring and summer, for reindeer it is the period of lowest documented captures in French sites, with their capture being more common in winter (Kuntz and Costamagno, 2011). However, as we have already mentioned, in the case of red deer it is more difficult to identify its catches in winter due to the disappearance of faunal indicators of this species in the Cantabrian region, something that also happens with reindeer in summer in the southwest of France (Fontana, 2017).

In relation to the catchment areas of macromammals, we have documented how red deer could be hunted in areas of relative proximity to almost all the sites (<5 km), and was mostly captured during the breeding and mating season of the animal. However, given the intense exploitation of this ungulate, it could be captured throughout the year in some sites such as Cualventi E, Linar 3C or Cierro G1. Regarding Iberian ibex and to a lesser extent chamois, although some deaths occurred during spring and summer, in the sites where there is a greater predominance of those animals (El Rascaño, El Mirón and Coímbre B), most of them were hunted in autumn and winter, coinciding with the lowest migration altitude of this species and the mating season. For the rest of the taxa, data on seasonal captures are very scarce, since the small number of individuals does not allow a clear pattern to be discerned in their captures.

From the calculation of the caloric energy that ungulates would have supplied to the human groups, red deer would have been the prey that would have contributed the greatest amount of meat and fat, exceeding 50% of the potential calories from these resources. Large prey, such as horse and large bovid, despite not being predominant in most of the sites, would have supplied 19.8% and 17% respectively of the potential meat resources to the lower Magdalenian groups. It should be noted that, despite being the predominant species in almost a third of the sites, the general energy contribution of Iberian ibex is < 10% and only in Arangas G and Erralla V was it the main energy source. The rest of the species would have contributed < 1% of the total calories.

In this way, in relation to the use of the environment and combining the data obtained in the palaeoecological and palaeoeconomic analyses, we have seen how red deer, bison and horses could be killed in a radius of about 2–3 km around most of the sites in the Cantabrian Spain, while in some cases the potential supply areas of Iberian ibex would be over 5 km away. Therefore, from an energy point of view, crag animals would only be more profitable where the orography favours their capture (Marín, 2010). If we add to this the high altitude migration system of these species, hunting red deer is seen to be much more profitable, placing it at the head of the energy contribution during the lower Magdalenian, given its greater caloric contribution to the group, its

lower acquisition cost, its high encounter rate and its handling time, especially in coastal valley areas. Even horse and large bovid could have been more profitable prey than Iberian ibex and chamois in deposits located near these coastal valleys, due to their greater energy contribution and the proximity of their catchment areas in places such as Las Caldas, Coímbre B or El Cierro. Furthermore, the encounter rate of larger animals such as horses or large bovids is much lower than that of medium-sized animals such as red deer, so in proportion a red deer would be sighted more often than a bison or a horse within the same ecosystem. Crag species would have been profitable only in sites with steep slopes and close to mountain areas such as Arangas, Erralla, Coímbre B or El Mirón, but even in some of these cases, red deer could provide greater caloric energy to the group.

Regarding the exploitation of the ecosystem, some researchers have assessed the risks of overexploitation of these ungulate species and the need to maintain mobility to allow the environment to regenerate (Stiner et al., 2008; Merkle et al., 2015; Venkataraman et al., 2017). In this sense, the increased hunting of red deer could have caused the occupation time of many of the sites in which this ungulate predominates to be potentially reduced depending on the type of exploitation of the environment. That is, if the animal exploitation strategy focuses on certain age groups, the regeneration times of the species will vary and the stay at the hunting site will be shorter. In those cases such as Cierro G1, Ekain VII, Erralla V, Riera 19, Linar 3C, Tito Bustillo 2 and Tito Bustillo 1, the abundant exploitation of hinds and their fawns does not allow prolonged capture of these resources over time, generating a process of ecosystem regeneration much slower than hunting strategies based on adult and senile specimens, as seems to occur for horse in the Las Caldas levels, or for red deer in La Güelga, Las Aguas or Cualventi. In this sense, logistical or even residential mobility (Binford, 1978) could generate a model that allows sustainable exploitation of the environment through a seasonal hunting cycle. Thus, we have seen how many of these caves present a relatively short seasonal occupation at different times of the year, which could have been oriented towards the regeneration of the environment in these intervals of seasonal occupation/disuse.

Taking this into account and from the data obtained on the caloric energy that the ungulates could have supplied to a hypothetical group of 10 individuals, for the lower Magdalenian, few levels would have allowed continuous occupation throughout a full year from these resources, which would imply that human groups would have to maintain wide mobility.

5. Conclusion

This research has characterized subsistence strategies in the Cantabrian Spain during the lower Magdalenian. From the palaeoecological, archaeozoological and taphonomic data of the faunal remains, we have been able to highlight the important role that red deer played in the subsistence of hunter-gatherer human groups; because it was not only one of the main species hunted and consumed, but also the largest energy resource in the meat diet of the inhabitants of the Cantabrian region during this period.

The combination of palaeoecological and palaeoeconomic analyses has demonstrated that the economic profitability of this species is not the only influencing factor in the hunting decisions made by human groups, but orographic aspects of the environment, the climate, the ethological behaviours of the animal to be hunted and its abundance in the environment in combination with the economic cost and benefit aspects of hunting were also important. This allows us to clarify the three site models proposed in the 1970s and that have been widely accepted for subsistence strategies in the region. However, it should always be taken into account that there are a series of unknowable aspects such as culinary tastes, food taboos or certain social aspects in consumption processes.

Within the three models, the "coastal model" includes those sites that

are located in valleys close to the current coastlines and where high percentages of red deer have been identified. Although this premise seems to be fulfilled during the lower Magdalenian, as high percentages of red deer are documented in those sites, it must be clarified that in some cases it would not have been the species that would have provided the greatest amount meat resources, as the greater size and profitability of prey like horse or large bovid would make them more important.

In the case of the "mountain model" that refers to sites located in mountainous areas or on steep slopes in which the presence of crag animals would be very abundant, the opposite occurs. Although Iberian ibex and chamois are the most common ungulates represented in these sites, bearing in mind the calories supplied by these resources during the lower Magdalenian, Iberian ibex is the main source of energy in only two levels (Erralla V and Arangas G). Therefore, although the orographic factor influences the capture, hunters would have attempted to optimize the energy contribution of the prey.

Finally, the "interior valley model" includes a series of sites located in valley areas distant from the coast, but close to different biotopes. They show greater diversification in the faunal spectrum in their sequences, as noted in La Güelga, Las Caldas, El Mirón or Arangas. These sites are generally located more than 17 km from the coast and have abundant catches of Iberian ibex and chamois, as well as red deer, and in some cases, horses and large bovids. In Las Caldas we have observed how in one level red deer is the most abundant prey, whereas horse predominates in the next. Important fluctuations are also observed in the predominance of red deer and Iberian ibex in Arangas and El Mirón. Although the available data has not allowed us to isolate a pattern that explains these changes, the greater or lesser representation of these species may be due to their abundance in the environment, ecological changes, and the seasonal occupation of the sites, which can produce an increase or decrease in catches of one species or another during different times. Although these factors have influenced the representation, as regards the energy contributed, once again the most profitable species in caloric terms are those that contributed the most to human groups in all periods, mainly red deer. This is indicative of the great economic profitability of this ungulate for the region, since it will always tend to be consumed and captured first, as long as its cost is not greater than the benefit provided by its capture.

This shows that, although the environment and the surrounding orography influence the subsistence strategy by determining the proximity and abundance of faunal resources, we must not ignore that human groups tend to consider the animals that are most economically profitable first, even though their cost is higher than that of others in the environment, since the energetic benefit offsets the expense of searching, capturing, and handling. This would explain how, in some sites such as Arangas or El Mirón, where Iberian ibex predominate based on the NISP, in the energy calculation red deer is the species that contributes the most. This strategy will be modified when the conditions under which these resources are profitable change, either due to variations in the abundance of the species in the environment, an increase in the cost or difficulty of acquiring them or changes in seasonal behaviour; or to avoid overexploitation of the resource. This would explain why in mountain places Iberian ibex and chamois are more profitable, but at sites in areas close to different biotopes, red deer and horses predominate in terms of energy contribution, despite the fact that smaller preys are more abundant and sometimes hunted more often.

CRediT authorship contribution statement

R. Portero: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Funding acquisition, Writing – original draft, Writing – review & editing. **M.J. Fernández-Gómez:** Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **E. Álvarez-Fernández:** Conceptualization, Formal analysis, Methodology, Funding acquisition, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2024.108651.

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APPENDIX 1: Supplementary information

Level	Date BP	Material	Method	Lab Code	Cal. BP 2σ	References
Aguas B	14550±60	AB	AMS	GrA-32757	18029 – 17449	
	14440±70	AB	AMS	GrA-30322	17866 – 17377	Rasines del Río, 2016
	15030±60	AB	AMS	GrA-32755	18631 – 18206	
Altamira 2	15910±230	C	Conv.	I-12012	19824 – 18790	González-Echegaray,1988;
	15420±70	AB	AMS	GrA-30329	18870 – 18363	Rasines del Río, 2016
Arangas F	15460±75	AB	AMS	OxA-27869	18901 – 18648	Álvarez-Fernández et al., 2020
Arangas G	15000±70	AB	AMS	OxA-36709	18630 – 18185	Álvarez-Fernández et al., 2020
Caldas XIII (Room II)	15165±160	AB	AMS	Ua-4301	18793 – 18216	Corchón, 2017
Caldas XIIi (Room II)	14835±130	AB	AMS	Ua-4300	18615 – 17790	Corchón, 2017
Caldas XII (Room II)	14495±140	AB	AMS	Ua-2735	18155 – 17340	Corchón, 2017;
	14811±54	AB	AMS	OxA-42390	18252 – 17966	This paper
Caldas XI (Room II)	13755±120	AB	AMS	Ua-2734	17025 – 16321	Corchón, 2017
Canes 2B	16560±210	AB	AMS	AA-12165	20501 – 19520	Arias, 2013
	15860±160	AB	AMS	OxA-7159	19514 – 18853	
Cierro F	15460±75	AB	AMS	OxA-27869	18901 – 18648	Álvarez-Fernández et al. 2016
Cierro G	15580±75	AB	AMS	OxA-27870	19011 – 19735	Álvarez-Fernández et al. 2016
Cierro G1	16360±55	SH	AMS	OxA-27871	19085 – 18655	Álvarez-Fernández et al. 2016
Coímbre B4	15710±60	AB	AMS	Beta-340005	19110 – 18855	Álvarez-Alonso y Jordá
	16440±70	AB	AMS	Beta-367726	20057 – 19587	Pardo, 2017
Cova Rosa B6	15810±60	SH	AMS	OxA-31708	18687 – 18158	Álvarez-Fernández et al.,
	15385±80	AB	AMS	OxA-38273	18860 – 18320	2019 y 2021
Cualventi E	14580±60	AB	AMS	GrA-27740	18109 – 17492	
	15450±70	AB	AMS	GrA-27741	18885 – 18650	Rasines del Río, 2016
	15420±70	AB	AMS	GrA-27742	18870 – 18363	
	15950±70	AB	AMS	GrA-27744	19471 – 19066	
Ekain VII	14183±88	-	AMS	Ua-40595	17438 – 17032	
	14919±91	-	AMS	Ua-38968	18620 – 17981	
	14605±92	-	AMS	Ua-40594	18175 – 17487	Altuna, 2012
	15592±108	-	AMS	Ua-40600	19101 – 18700	
	14143±97	-	AMS	Ua-40599	17426 – 16987	
	15447±122	-	AMS	Ua-40598	18971 – 18308	
Erralla V	15740±240	AB	Conv.	I-12540	19592 – 18633	Altuna, 1985
Güelga 3	14020±130	AB	Conv.	GrN-17255	17384 – 16642	Menéndez et al., 2005
	14090±190	AB	Conv.	GrN-1610	17775 – 16579	This paper
	14750±54	AB	AMS	OxA-42392	18224 – 17899	
Juyo 7	14440±180	-	Conv.	I-10738	18144 – 17127	González-Echegaray, 1987
Juyo 4	13920±240	-	Conv.	I-10736	17545 – 16165	González-Echegaray, 1987
Linar 3C	15420 ± 70	AB	AMS	GrA-27748	18870 – 18363	Rasines del Río, 2016
	15860 ± 70	AB	AMS	GrA-33148	19372 – 18943	
	14040 ± 60	AB	AMS	GrA-27750	17337 – 16938	
Mirón 115 (vestibule rear)	16750 ± 45	AB	AMS	UG-31472	20420–20100	Hopkins et al., 2020
Mirón 504 (burial)	15460 ± 40	HB	AMS	MAMS-14585	18847 – 18696	Marín y Geiling, 2015
	15740 ± 40	AB	AMS	UGA-7217	19109 – 18893	
Rascaño 5	16433 ± 131	AB	Conv.	B.M. 1455	20196 – 19528	Barandiarán y González-Echegaray, 1981
Rascaño 4	15988 ± 193	AB	Conv.	B.M. 1453	19820 – 18878	Barandiarán y González-Echegaray, 1981
Rascaño 3	15173 ± 160	AB	Conv.	B.M. 1452	18785 – 18220	Barandiarán y González-Echegaray, 1981
Riera 19	16420 ± 430	C	Conv.	Gak-6448	20875 – 18889	Straus, 1986
	15520 ± 350	C	Conv.	Q-2110	19623 – 18164	
	15230 ± 300	C	Conv.	Q-2116	19177 – 17867	
Santimamiñe Csn-Camr	14650± 80	AB	AMS	Beta-240905	18209 – 17584	López Quintana y Guenga, 2011
	14670 ± 80	AB	AMS	Beta-240904	18225 – 17721	
Tito Bustillo 1	15175±50	SH	AMS	OxA-29095	18015 – 17360	Álvarez-Fernández et al., 2015
	15150±50	SH	AMS	OxA-29076	17990 – 17335	
	15570±55	SH	AMS	OxA-29117	18497 – 17851	
Tito Bustillo 2	14890±410	AB	Conv.	Ly-4212	19000 – 17092	Moure, 1997

Table 1: Radiocarbon dates for the lower Magdalenian levels, indicating the material that was dated, the lab code, radiocarbon age (BP) and calibrated date (cal. BP) to 2σ at 95.4%, obtained with the IntCal20 curve (Reimer et al., 2020), Marine 20 curve (Heaton et al., 2020) and the OxCal v.4.4. programme. The reservoir effect of 117 ± 70 established for the Cantabrian Sea (Monge Soares et al., 2016) was employed in the case of the marine sample. C=charcoal; AB=Animal bone; HB=Human bone; SH=Shell.

Level	NISP	%NISP-DTaxon	NTaxa	D	1-D	1/D	H'	E	LN NISP	Log. NISP	qD	References
Cierro G1	2592	CE-91,2	6	0,84	0,16	1,19	0,39	0,25	7,85	3,41	1,48	This work
Cierro G	558	CE-91,2	5	0,84	0,16	1,19	0,38	0,29	6,32	2,75	1,46	Portero et al., 2019
Cierro F	1076	CE-92,4	4	0,86	0,14	1,16	0,31	0,34	6,98	3,03	1,36	Álvarez-Fernández et al., 2016
Cova Rosa B6	170	CE-85,9	5	0,75	0,25	1,33	0,51	0,33	5,13	2,23	1,66	Álvarez-Fernández et al., 2019
Tito Bustillo 2	441	CE-94,7	5	0,9	0,1	1,11	0,27	0,26	6,09	2,64	1,31	Altuna, 1976
Tito Bustillo 1c	1443	CE-84,7	9	0,73	0,27	1,37	0,59	0,20	7,27	3,16	1,80	Altuna, 1976
Tito Bustillo 1b	1344	CE-79	7	0,64	0,36	1,55	0,75	0,30	7,2	3,13	2,11	Altuna, 1976
Tito Bustillo 1a	1071	CE-77,9	7	0,63	0,37	1,59	0,80	0,31	6,98	3,03	2,23	Altuna, 1976
Güelga 3	1001	CE-63,6	8	0,48	0,52	2,09	0,96	0,33	6,91	3	2,62	Rojo, 2020
Caldas XIII	93	CE-79,6	5	0,65	0,35	1,55	0,75	0,43	4,53	1,97	2,13	Altuna and Mariezkurrena, 2017
Caldas XII	1118	EQ-50	8	0,45	0,55	2,21	0,92	0,31	7,02	3,05	2,51	Altuna and Mariezkurrena, 2017
Caldas XIIi	323	CE-61	10	0,43	0,57	2,31	1,16	0,32	5,78	2,51	3,18	Altuna y Mariezkurrena, 2017
Caldas XI	663	EQ-49	8	0,42	0,58	2,40	1,03	0,35	6,5	2,82	2,81	Altuna and Mariezkurrena, 2017
Coímbre B4	371	CA-67,5	5	0,52	0,48	1,94	0,94	0,51	5,92	2,57	2,55	Yravedra et al., 2017
Canes 2B	59	CA-68,6	5	0,51	0,49	1,97	0,97	0,53	4,08	1,77	2,63	Arias, 2002
Arangas F	205	CA-64,2	6	0,33	0,67	3,01	1,29	0,60	5,32	2,31	3,63	Álvarez-Fernández et al., 2020
Arangas G	67	CA-43,4	4	0,47	0,53	2,12	0,95	0,65	4,2	1,83	2,59	Álvarez-Fernández, et al., 2020
Riera 19	1704	CE-77,6	5	0,65	0,35	1,54	0,56	0,35	7,44	3,23	1,75	Altuna, 1986
Mirón 115	553	CA-46,8	7	0,42	0,58	2,39	1,05	0,41	6,32	2,74	2,86	Carvalho et al., 2021
Mirón 504	614	CA-62,9	6	0,52	0,48	1,93	0,77	0,36	6,42	2,79	2,16	Marín and Geiling, 2015
Ekain VII	807	CE-85,1	10	0,66	0,34	1,51	0,79	0,22	6,69	2,91	2,20	Altuna and Mariezkurrena, 1984
Erralla V	2677	CE-88,7	10	0,79	0,21	1,26	0,45	0,16	7,89	3,43	1,57	Altuna and Mariezkurrena, 1985
Rascaño 5	1655	CA-79	8	0,65	0,35	1,54	0,71	0,26	7,41	3,22	2,04	Altuna, 1981
Rascaño 4	2476	CA-81	10	0,66	0,34	1,51	0,70	0,20	7,81	3,39	2,01	Altuna, 1981
Rascaño 3	547	CA-93	6	0,87	0,13	1,15	0,31	0,23	6,30	2,74	1,37	Altuna, 1981
Santimamiñe Csn-Camr	280	CE-91,1	6	0,83	0,17	1,20	0,40	0,25	5,63	2,45	1,49	Castaños and Castaños, 2011
Juyo 7	153	CE-91,5	5	0,84	0,16	1,19	0,37	0,29	5,03	2,18	1,45	Klein and Cruz Uribe, 1987
Juyo 4	2378	CE-90,4	10	0,82	0,18	1,22	0,47	0,16	7,77	3,38	1,60	Klein and Cruz Uribe, 1987
Cualventi E	2986	CE-93,6	9	0,88	0,12	1,14	0,34	0,16	8,00	3,48	1,41	Castaños, 2016
Linar 3c	344	CE-87	10	0,74	0,26	1,34	0,66	0,19	5,84	2,54	1,94	Castaños, 2016
Aguas B	778	CE-95,7	6	0,92	0,08	1,09	0,22	0,21	6,66	2,89	1,25	Castaños, 2016
Altamira 2	2277	CE-95,1	8	0.91	0,06	1,10	0,27	0,16	7,73	3,36	1,31	Castaños and Castaños, 2014

Table 2: Palaeoecological data of the selected lower Magdalenian levels. NTaxa = Number of taxa identified in the level. %NISP-DTaxon= Percentage of NISP of dominant taxon (CE=*Cervus elaphus*, CA=*Capra pyrenaica*; EQ=*Equus ferus*). D= Simpson's index. 1-D= Simpson's diversity index. 1/D= Simpson's reciprocal index. Shannon index. E = Evenness. LN NISP= Napierian Logarithm of NISP. Log. NISP: Natural Logarithm of NISP. *qD* = Effective Number of Species.

Taxon	Level	Age Cat.	Middle weight (Kg)	Meat + fat (Kg)	Energy (Kcal/ Kg)	MNI	Total Meat+fat (Kg)	Total Energy (Kcal)	References
Cervus elaphus	Arangas F	AD	93,5	36,7	1.110	2	73,4	81.474	Clutton-Brock and Iason, 1986; Marín, 2010; Carranza, 2017
		JU	62,4	24,5	1.110	1	24,5	27.195	
	Cierro G1	AD	93,5	36,7	1.110	28	1027,6	1.140.636	
		JU	62,4	24,5	1.110	8	196	217.560	
		IMM	31,1	12,2	1.110	11	134,2	148.962	
	Cierro G	AD	93,5	36,7	1.110	7	256,9	285.159	
		JU	62,4	24,5	1.110	1	24,5	27.195	
		IMM	31,1	12,2	1.110	3	36,6	40.626	
	Cierro F	AD	93,5	36,7	1.110	5	183,5	203.685	
		JU	62,4	24,5	1.110	1	24,5	27.195	
		IMM	31,1	12,2	1.110	2	24,4	27.084	
	Coímbre B4	AD	93,5	36,7	1.110	2	73,4	81.474	
	Cova Rosa B6	AD	93,5	36,7	1.110	5	183,5	203.685	
		IMM	31,1	12,2	1.110	2	24,4	27.084	
	Cualventi E	AD	93,5	36,7	1.110	38	1.394,6	1.548.006	
		JU	62,4	24,5	1.110	8	196	217.560	
		IMM	31,1	12,2	1.110	8	97,6	108.336	
	Ekain VII	AD	93,5	36,7	1.110	6	220,2	244.422	
		IMM	31,1	12,2	1.110	18	219,6	243.756	
	Linar 3C	AD	93,5	36,7	1.110	13	447,1	529.581	
		JU	62,4	24,5	1.110	6	147	163.170	
		IMM	31,1	12,2	1.110	6	73,2	81.252	
	Erralla V	IMM	31,1	12,2	1.110	5	61	67.710	
	Güelga 3	AD	93,5	36,7	1.110	10	367	407.370	
		IMM	31,1	12,2	1.110	3	36,6	40.626	
	Riera 19	AD	93,5	36,7	1.110	11	403,7	448.107	
		JU	62,4	24,5	1.110	10	254	281.940	
		IMM	31,1	12,2	1.110	2	24,4	27.084	
	Aguas B	AD	93,5	36,7	1.110	10	36,6	40.626	
		JU	62,4	24,5	1.110	3	73,5	81.585	
		IMM	31,1	12,2	1.110	2	24,4	27.084	
	Caldas XIII	AD	93,5	36,7	1.110	3	110,1	122.211	
		IMM	31,1	12,2	1.110	1	12,2	13.542	
	Caldas XIIi	AD	93,5	36,7	1.110	6	220,2	244.422	
		JU	62,4	24,5	1.110	1	24,5	27.195	
	Caldas XII	AD	93,5	36,7	1.110	6	220,2	244.422	
		JU	62,4	24,5	1.110	2	49	54.390	
	Caldas XI	AD	93,5	36,7	1.110	5	183,5	203.685	
		JU	62,4	24,5	1.110	1	24,5	27.195	
		IMM	31,1	12,2	1.110	1	12,2	13.542	
	Mirón 504	AD	93,5	36,7	1.110	2	73,4	81.474	
		JU	62,4	24,5	1.110	2	49	54.390	
	Santimamiñe Csn-Camr	AD	93,5	36,7	1.110	3	110,1	122.211	
Capra pyrenaica	Arangas F	AD	51,2	19,4	1.140	1	19,4	22.116	Marín, 2010; Alados and Escós, 2017
		JU	34,2	13	1.140	1	13	14.820	
	Arangas G	AD	51,2	19,4	1.140	2	38,8	44.232	
		JU	34,2	13	1.140	2	26	29.640	
	Cierro G1	AD	51,2	19,4	1.140	4	77,6	88.464	
		JU	34,2	13	1.140	1	13	14.820	
		IMM	17	6,4	1.140	1	6,4	7.296	
	Cierro G	AD	51,2	19,4	1.140	1	19,4	22.116	
		JU	34,2	13	1.140	1	13	14.820	
	Cierro F	AD	51,2	19,4	1.140	2	38,8	44.232	
	Coímbre B4	AD	51,2	19,4	1.140	8	155,2	176.928	
		IMM	17	6,4	1.140	1	6,4	7.296	
	Ekain VII	AD	51,2	19,4	1.140	4	77,6	88.464	
		IMM	17	6,4	1.140	2	12,8	14.592	
	Erralla V	AD	51,2	19,4	1.140	4	77,6	88.464	
		JU	34,2	13	1.140	7	91	103.740	
		IMM	17	6,4	1.140	11	70,4	80.256	
	Güelga 3	AD	51,2	19,4	1.140	8	155,2	176.928	
		IMM	17	6,4	1.140	2	12,8	14.592	
	Riera 19	AD	51,2	19,4	1.140	5	97	110.580	
		JU	34,2	13	1.140	2	26	29.640	
	Caldas XI	AD	51,2	19,4	1.140	2	38,8	44.232	
		JU	34,2	13	1.140	1	13	14.820	
		IMM	17	6,4	1.140	1	6,4	7.296	

Continuation table 3

	Mirón 504	AD	51,2	19,4	1.140	3	58,2	66.348	
		JU	34,2	13	1.140	4	52	59.280	
Rupicapra pyrenaica	Arangas F	AD	26,5	10	1.140	1	10	11.400	Marín, 2010; Pérez-Barbería et al., 2017
		JU	17,7	6,7	1.140	1	6,7	7.638	
	Coímbre B4	AD	26,5	10	1.140	2	20	22.800	
		IMM	8,8	3,3	1.140	2	6,6	7.524	
	Ekain VII	AD	26,5	10	1.140	2	20	22.800	
		JU	17,7	6,7	1.140	2	13,4	15.276	
	Güelga 3	AD	26,5	10	1.140	5	50	57.000	
		JU	17,7	6,7	1.140	2	13,4	15.276	
Capreolus capreolus	Arangas G	JU	16,3	6,3	1.110	1	6,3	6.993	Marín, 2010; Mateos-Quesada, 2011
	Cierro G1	AD	24,4	9,5	1.110	3	28,5	31.635	
		IMM	8,1	3,2	1.110	1	3,2	3.552	
	Cierro F	AD	24,4	9,5	1.110	2	19	21.090	
	Güelga 3	AD	24,4	9,5	1.110	1	9,5	10.545	
	Riera 19	AD	24,4	9,5	1.110	1	9,5	10.545	
Bos/Bison	Cierro G1	AD	600	300	1.220	2	600	732.000	Krasinska and Krasinski, 2002; Marín, 2008a; USDA, 2020
		IMM	199,8	100	1.220	1	100	122.200	
	Cierro G	AD	600	300	1.220	1	300	366.000	
	Cierro F	AD	600	300	1.220	1	300	366.000	
	Coímbre B4	AD	600	300	1.220	2	600	732.000	
	Caldas XIII	AD	600	300	1.220	1	300	366.000	
Equus ferus	Cierro G1	AD	210,25	147,1	1.080	1	147,1	158.868	Outram and Rowley-Conwy, 1998; USDA, 2020
	Coímbre B4	IMM	70,1	49	1.080	1	49	52.920	
	Riera 19	AD	210,25	147,1	1.080	1	147,1	158.868	
	Caldas XIII	AD	210,25	147,1	1.080	2	294,2	317.736	
	Caldas XII	AD	210,25	147,1	1.080	9	1.329,3	1.429.812	
		JU	140,2	98,1	1.080	1	98,1	105.948	
	Caldas XIIi	AD	210,25	147,1	1.080	3	441,3	476.604	
	Caldas XI	AD	210,25	147,1	1.080	2	294,2	317.736	
		JU	140,2	98,1	1.080	1	98,1	105.948	

Table 3: Caloric energy provided by taxon and age category of the macromammal species documented in the lower Magdalenian levels of the Cantabrian region, based on the average weight of both sexes and the proportion of meat and fat provided by each individual per age category.
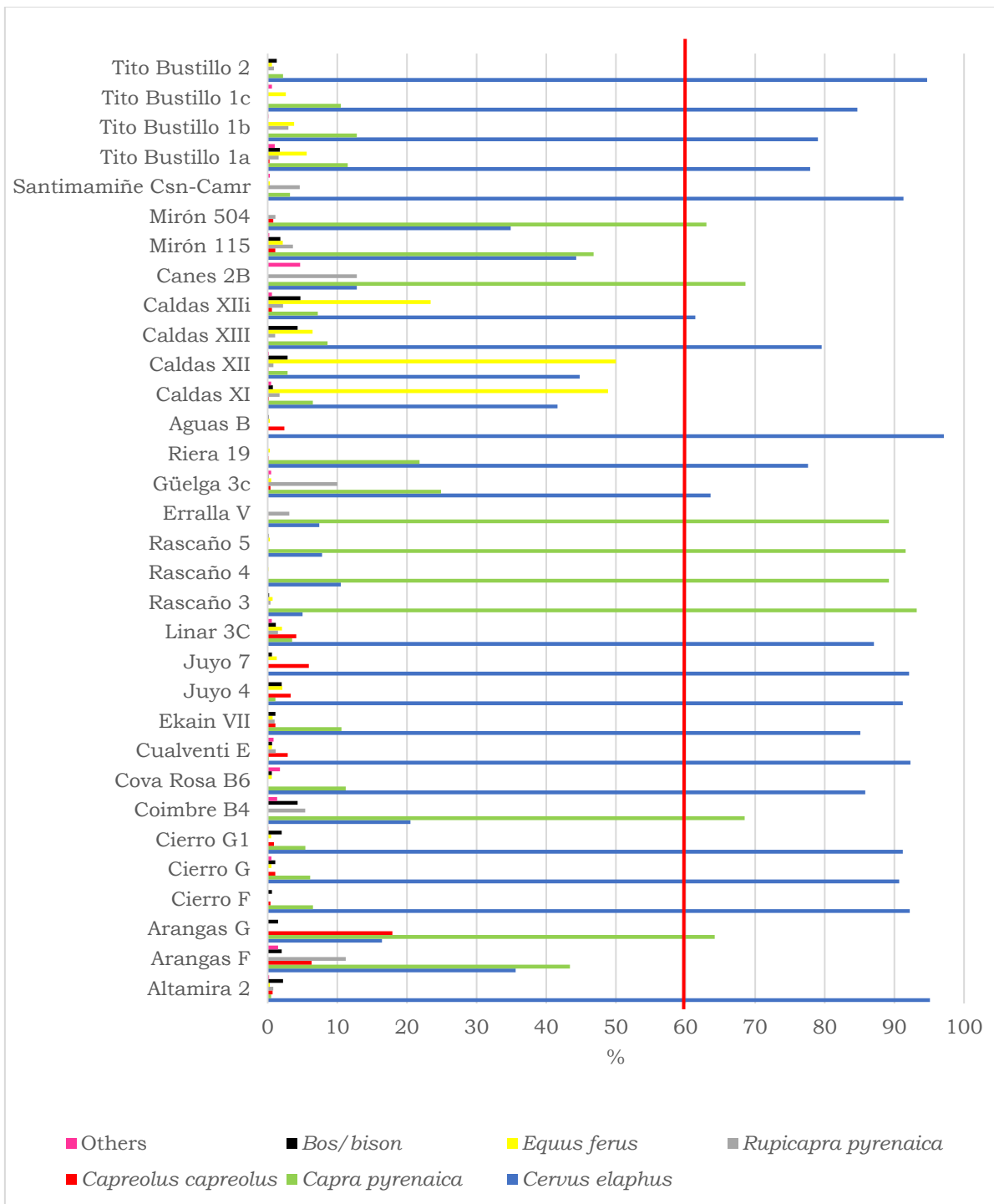
Figure 1: Percentage of taxonomical representation (from NISP) of macromammals documented in the lower Magdalenian levels in Cantabrian Spain. Red line represents 60%, the umbral at which the predominance of a taxon can be established (Yravedra, 2002a).
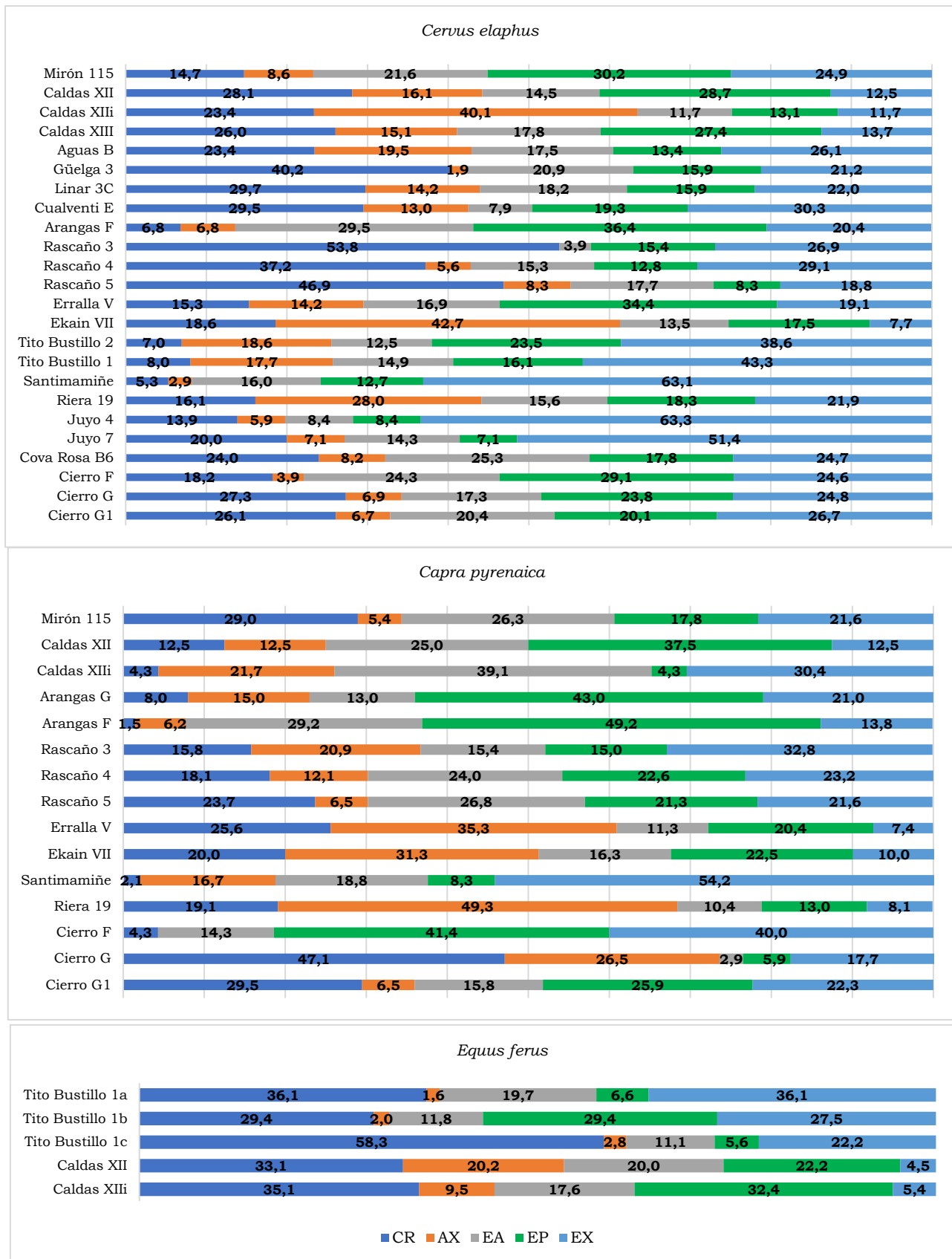
Figure 2: Percentage of skeletal representation of prey documented in the lower Magdalenian levels of the Cantabrian region (CR=cranial; AX=axial; EA=forelimb; EP=hindlimb; EX=limb). Taxa with fewer than twenty remains have not been represented.
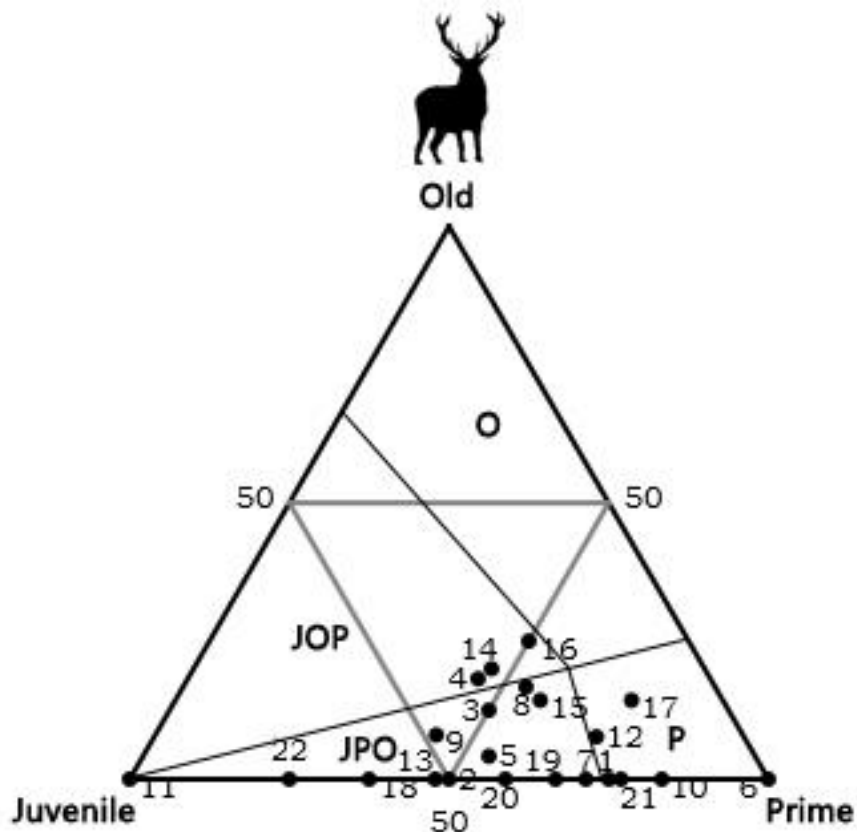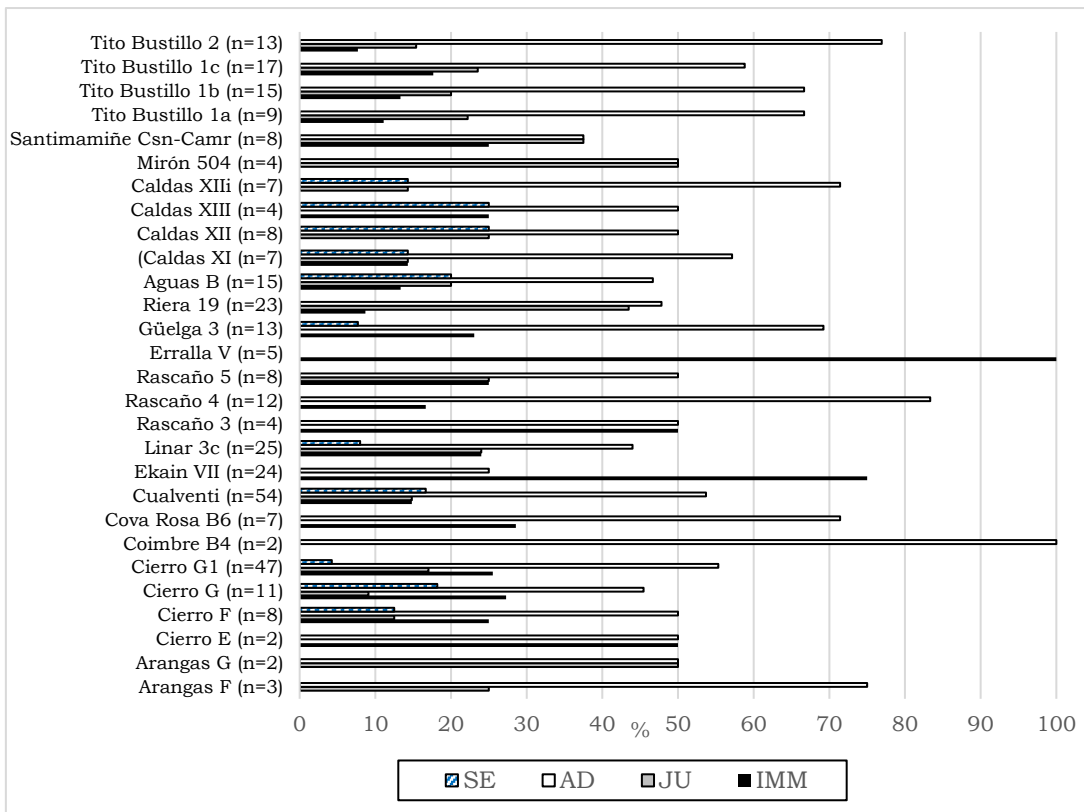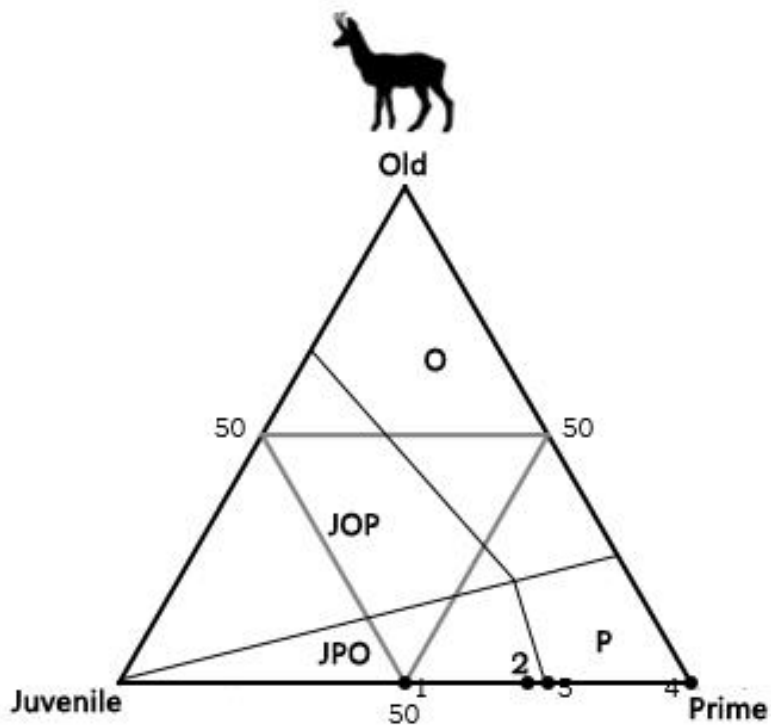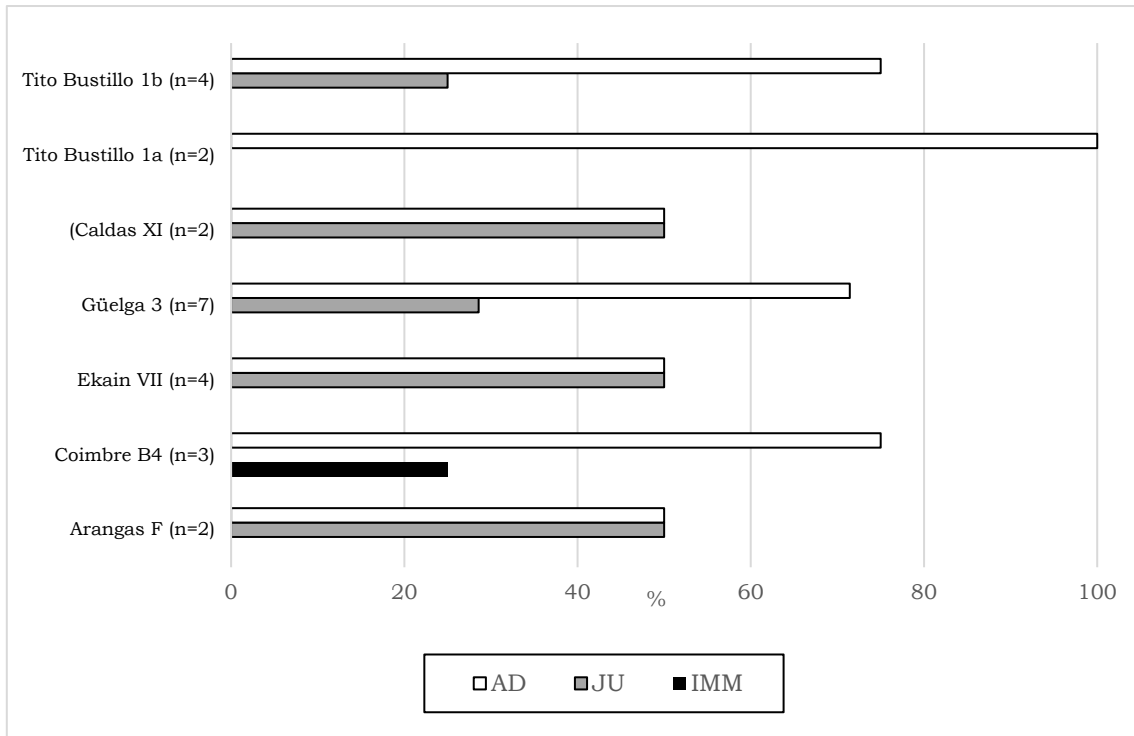
Figure 3: Percentage of age categories of lower Magdalenian red deer in Cantabrian Spain and ternary distribution chart according to zones established by Discamps and Costamagno (2015). 1) Arangas F; 2) Arangas G, Cierro E, Rascaño 3, Mirón 504; 3) Cierro F; 4) Cierro G; 5) Cierro G1; 6) Coímbre B4; 7) Cova Rosa B4; 8) Cualventi E; 9) Linar 3C; 10) Rascaño 4; 11) Erralla V; 12) Güelga 3; 13) Riera 19; 14) Aguas B; 15) Caldas XI; 16) Caldas XII y XII; 17) Caldas XIIi; 18) Santimamiñe Csn-Camr; 19) Tito Bustillo 1a y 1b; 20) Tito Bustillo 1c; 21) Tito Bustillo 2; 22) Ekain. IMM: Immature; JU: juvenile; AD: adult; SE: senile. Levels with a single individual are not represented.
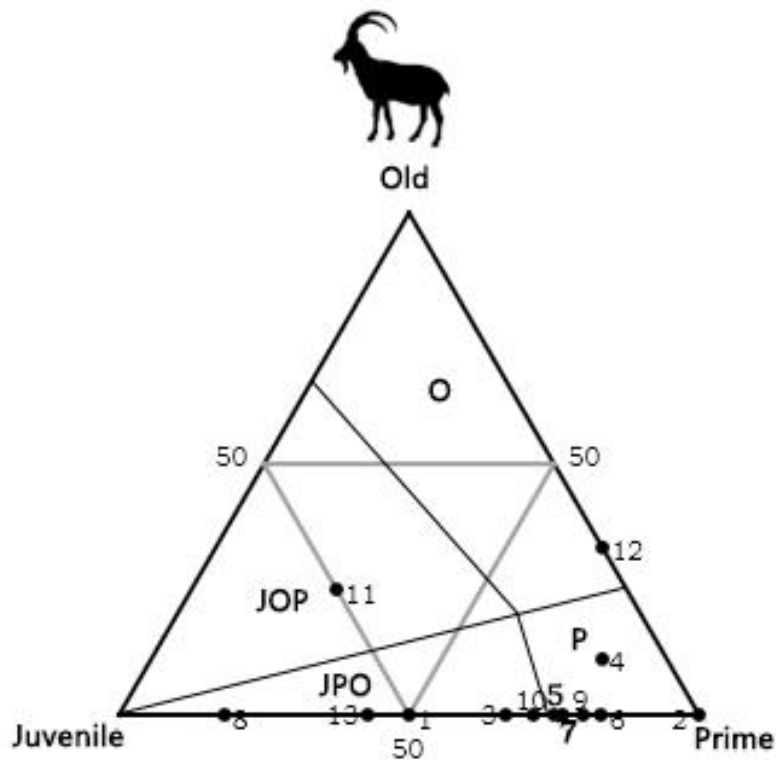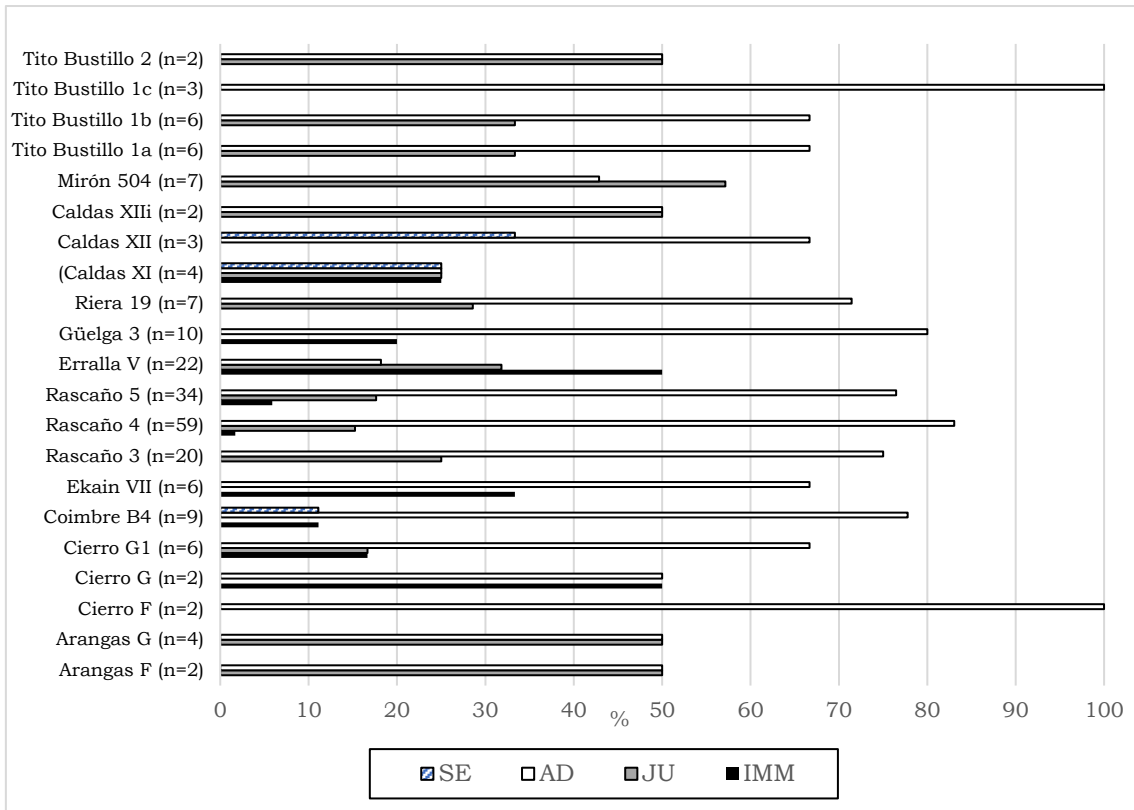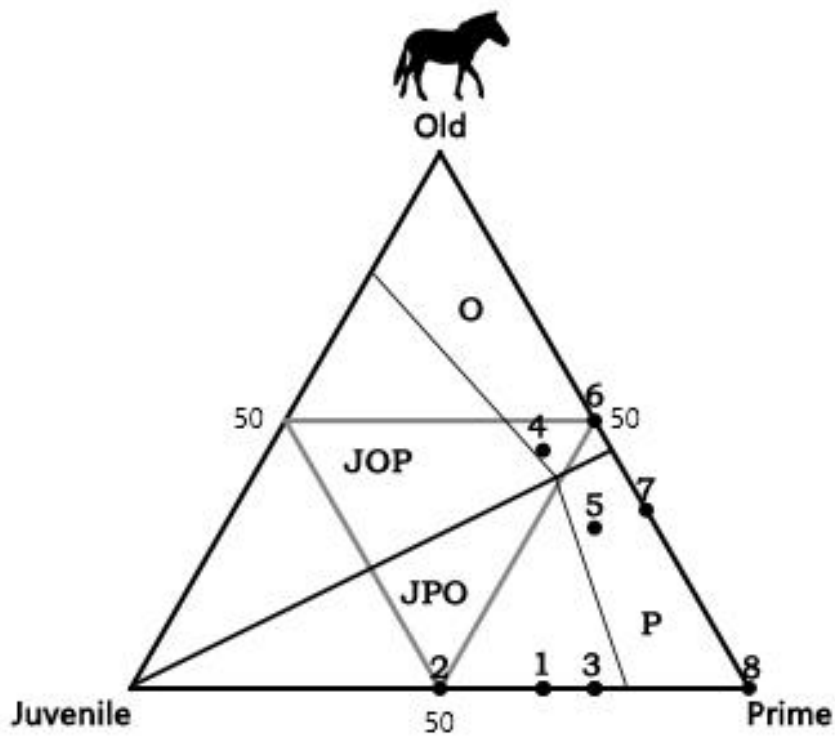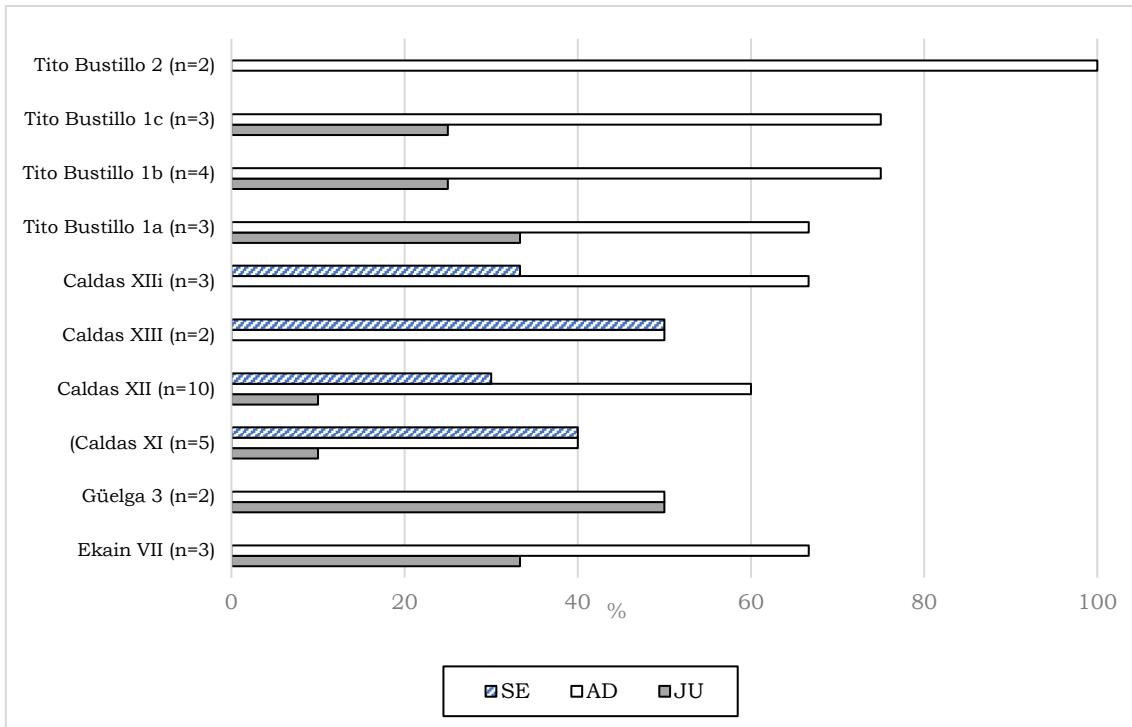
Figure 4: Percentage of age categories of lower Magdalenian Iberian ibex in Cantabrian Spain and ternary distribution chart according to zones established E. Discamps and Costamagno (2015). 1) Arangas G y F, Cierro E, Caldas XIIi, Tito Bustillo 2; 2) Cierro F, Tito Bustillo 1c; 3) Cierro G1, Tito Bustillo 1a y 1b, Ekain VII. 4) Coímbre B4; 5) Rascaño 3; 6) Rascaño 4; 7) Rascaño 5; 8) Erralla V; 9) Güelga 3; 10) Riera 19; 11) Caldas XI; 12) Caldas XII; 13) Mirón 504. IMM: Immature; JU: juvenile; AD: adult; SE: senile. Levels with a single individual are not represented.
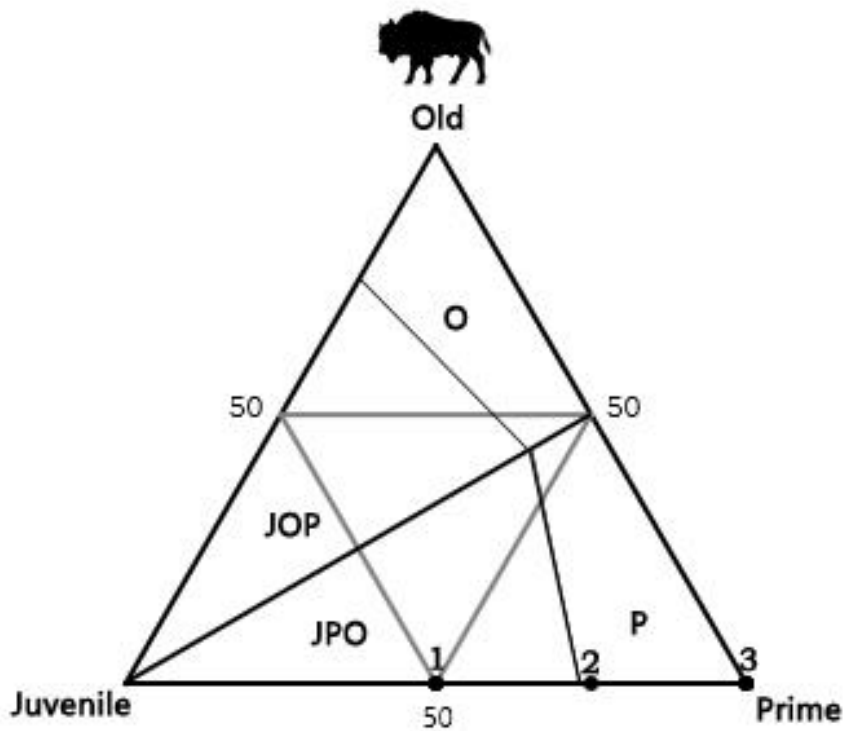
Figure 5: Percentage of age categories of lower Magdalenian chamois in Cantabrian Spain and ternary distribution chart according to zones established by Discamps and Costamagno (2015). 1) Arangas F, Ekain VII, Caldas XI; 2) Güelga 3; 3) Coímbre B4, Tito Bustillo 1b; 4) Tito Bustillo 1a. IMM: Immature; JU: juvenile; AD: adult; SE: senile. Levels with a single individual are not represented.

Figure 6: Percentage of age categories of lower Magdalenian horse in Cantabrian Spain and ternary distribution chart according to zones established by Discamps and Costamagno (2015). 1) Ekain VII, Tito Bustillo 1a; 2) Güelga 3; 3) Tito Bustillo 1b y 1c; 4) Caldas XI; 5) Caldas XII; 6) Caldas XIII; 7) Caldas XIIi; 8) Tito Bustillo 2. IMM: Immature; JU: juvenile; AD: adult; SE: senile. Levels with a single individual are not represented.
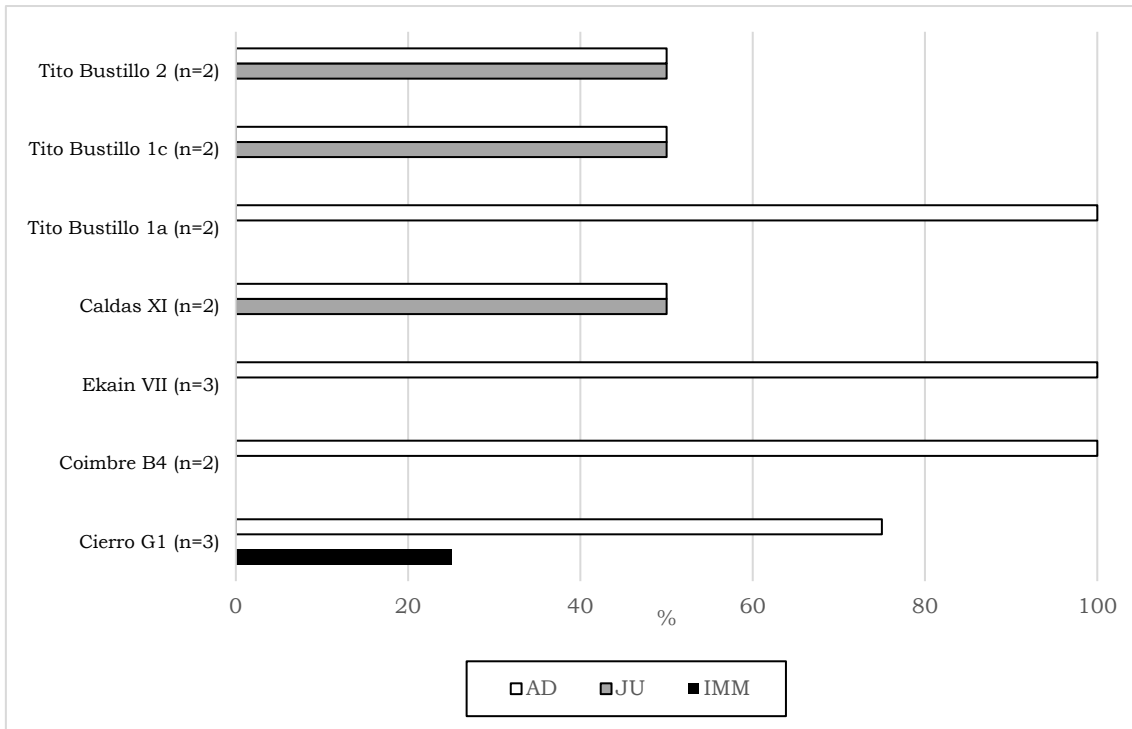
Figure 7: Percentage of age categories of lower Magdalenian bison in Cantabrian Spain and ternary distribution chart according to zones established by Discamps and Costamagno (2015). 1) Las Caldas XI, Tito Bustillo 1c y 2; 2) Cierro G1; 3) Coímbre B4, Ekain VII, Tito Bustillo 1a. IMM: Immature; JU: juvenile; AD: adult; SE: senile. Levels with a single individual are not represented.
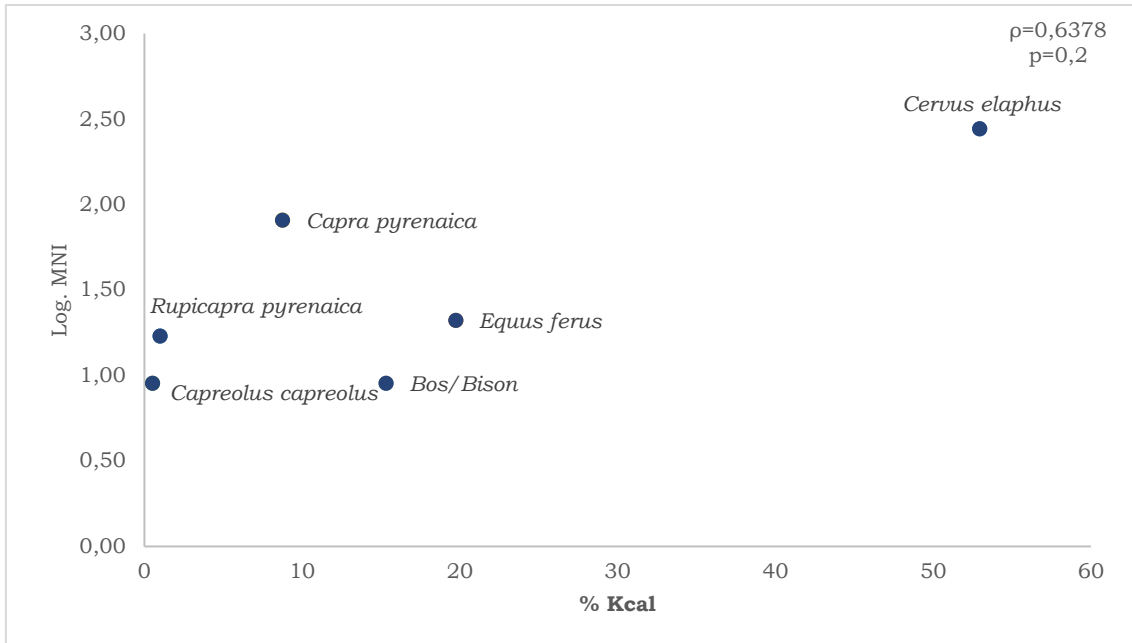
Figure 8: Correlation between the percentage of energy contributed by each taxon and the representation of each species (Log. MNI) during the ñower Magdalenian of the Cantabrian region.
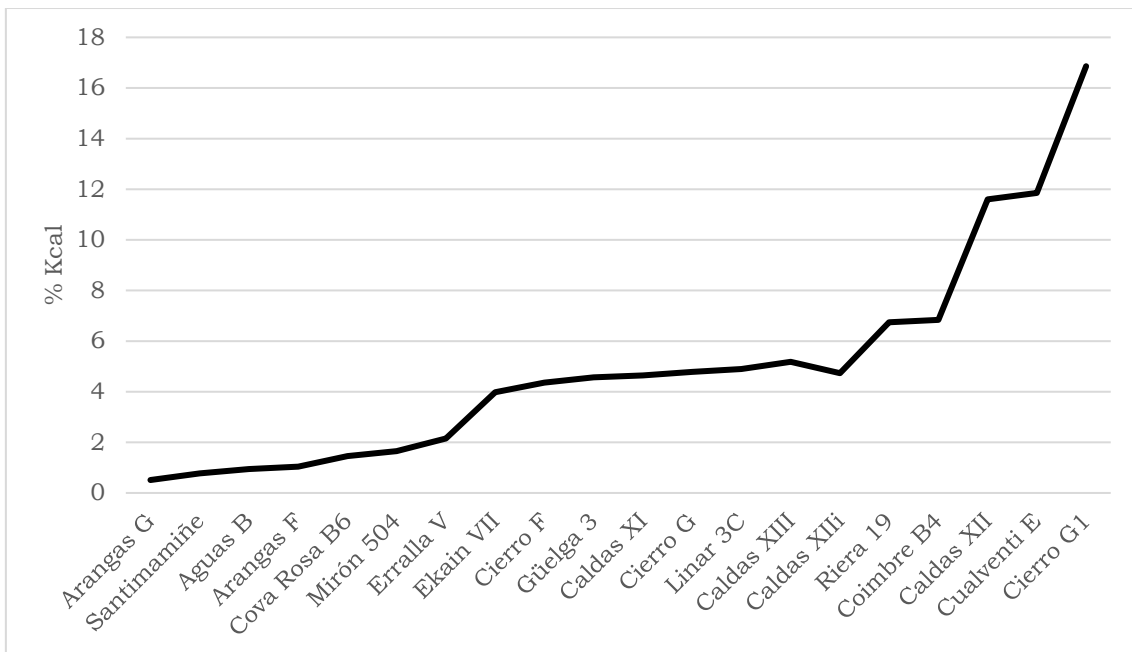

Figure 9: Percentage of total calories provided by each level of the lower Magdalenian of the Cantabrian region in ascending order.
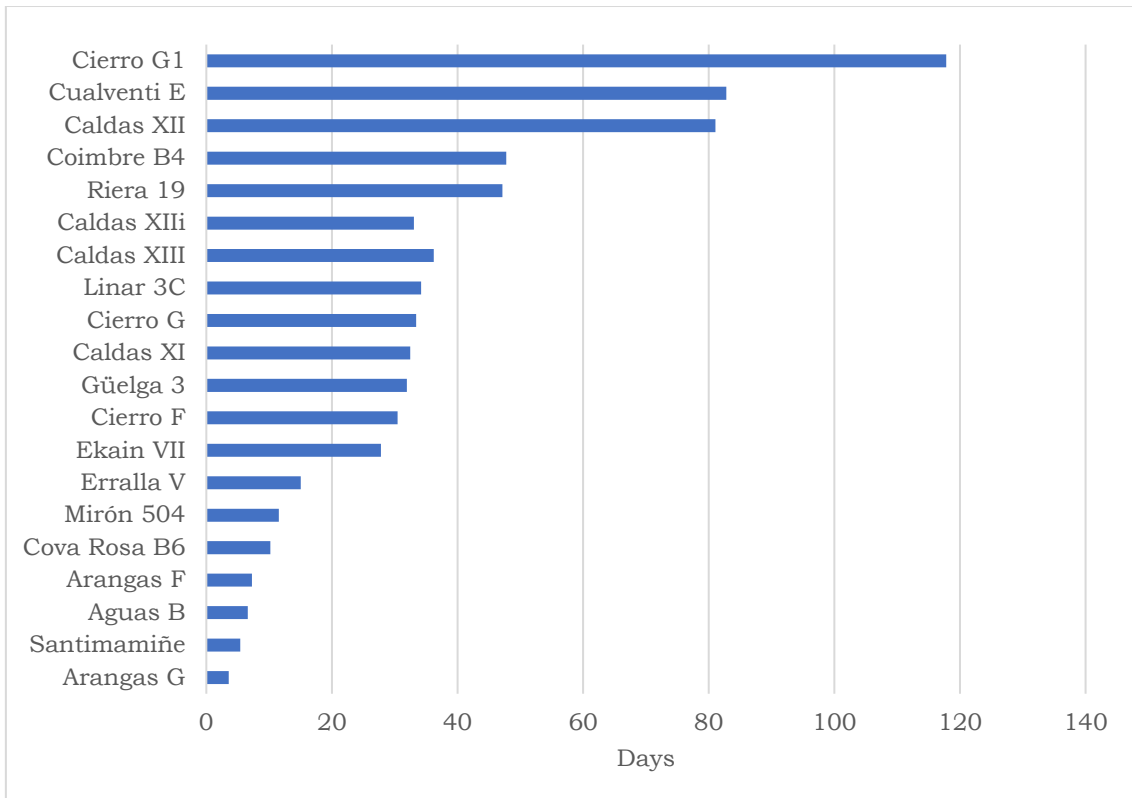
Figure 10: Hypothetical reconstruction of the total number of days that could have been fed by the faunal resources documented in the lower Magdalenian sites for a group of 10 adults, calculated from the average daily energy expenditure of the Hadza (Pontzer et al., 2012).