Journal of Archaeological Science: Reports 71 (2026) 105704

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

Livestock feeding strategies through the seasons: Isotopic evidence from the Late Iron Age site of Mas Castellar de Pontós (Girona, Catalonia)☆

Messana Chiara [a,b,*], Tornero Carlos [a,b], Pons Enriqueta [c], Colominas Lídia [d]

[a] Department of Prehistory, Autonomous University of Barcelona (UAB), (ES), Bellaterra, Spain
[b] Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), (ES), Tarragona, Spain
[c] MAC-Girona, (ES), Girona, Spain
[d] Institut Català d'Arqueologia Clàssica (ICAC-CERCA), (ES), Tarragona, Spain

ARTICLE INFO

Keywords:
Livestock diet
Stable isotopes
Sequential $\delta^{13}C$ and $\delta^{18}O$ analysis
Iron Age husbandry
NE Iberian Peninsula

ABSTRACT

This study investigates cattle feeding strategies at the Late Iron Age rural establishment of Mas Castellar de Pontós (Empordà plain, northeastern Iberian Peninsula), a key agricultural and commercial centre linked to the coastal Greek colonies of Emporion and Rhode. Previous isotopic data from bulk collagen analyses of bones (Messana et al. 2025) suggested a potential introduction of C_4 plants into the cattle diet; however, the temporal dimensions of this practice remained unclear. To address this gap, sequential analyses of $\delta^{13}C$ and $\delta^{18}O$ values were performed on dental enamel from seven lower molars belonging to five cattle, allowing a seasonal resolution of their feeding habits.

The results confirm the seasonal integration of C_4 plants into the cattle diet during the warmer months, complementing a basal C_3 plant consumption during the year. Considering the landscape surrounding the settlement and the agricultural activity, two options are proposed regarding the nature of the C_4 plants consumed: cultivated cereals such as millet or wild plants growing along the coast and in salt marshes. The isotopic data currently available do not allow a discernment between the two hypotheses, resulting in a scenario of so-called equifinality.

This pattern reflects a deliberate and seasonally adaptive feeding strategy, comparable to that observed in sheep from the same settlement. This evidence suggest that cattle, as has been documented for sheep, had access to a diversified range of plant resources during the year. These livestock feeding habits may have been adopted by herders to maximise the availability of pasture and/or fodder.

1. Introduction

1.1. Research context

During the Late Iron Age (3rd-2nd c. BC), Iberian communities were organised around central nuclei, the first-order cities, creating a network of interconnected open-air centres. Each of these settlements had specific functions and characteristics: fortified centres, rural establishments, small villages, and silo fields (Gracia, 2005; Sanmartí, 2014, 2021). The subsistence strategies of these communities were based on peasant economies, devoted to self-sufficiency and strongly related to the ecological conditions of each settlement. In this scenario, the settlement of Mas Castellar de Pontós played a prominent role as a rural economic centre (Pons et al., 2010).

Mas Castellar de Pontós (MC) is situated in the northeast of the Iberian Peninsula, on a fertile plain in the Empordà region (Girona, Catalonia, 154 m a.s.L.; Fig. 1a), near the Mediterranean coast. The site is located on a promontory between two watercourses, approximately 17 km from the Greek colonies of *Rhode* and *Emporion*. The fertile territory and the humid, temperate climate played a significant role in the flourishing of agricultural activities, particularly in cereal production. Furthermore, the favourable geographic position enabled the settlement to become an important and strategic hub of communication between the coastal Greek colonies and the indigenous communities of the inland (Pons et al., 2010). Contacts with coastal regions are reflected in the presence of imported Greek, Etruscan, and Punic ceramics, both luxury

☆ This article is part of a special issue entitled: 'Iberian Zooarchaeology' published in Journal of Archaeological Science: Reports.

* Corresponding author.
E-mail addresses: cmessana@iphes.cat, Chiara.Messana@uab.cat (M. Chiara).

https://doi.org/10.1016/j.jasrep.2026.105704
Received 31 October 2025; Received in revised form 7 March 2026; Accepted 12 March 2026
Available online 21 March 2026

and cooking ware, as well as in transport amphorae. The cereal surplus was the main reason for maintaining Mediterranean trade (Bouso et al., 2002; Pons et al., 2010).

The archaeological complex, extending across approximately 5 ha, stretches over two plains: an upper one, known as 'Camp de Dalt', and a lower one, identified as 'Camp de Baix' (Fig. 1b). Human occupation of the settlement covers a wide chronological spectrum, spanning from the late 9th century BCE (Period I, 850–700 BCE) to the early 2nd century BCE (Period VI, 180–170 BCE; Adroher and Pons, 2002; Pons et al., 2010).

1.2. The rural establishment

The phase investigated here corresponds to Period V (250–180 BCE), during which the site was occupied by the so-called rural establishment (Fuertes et al., 2002; Pons et al., 2010; Fig. 2). Situated on the east side of the 'Camp de Dalt', this specialised agricultural settlement was controlled by a rural aristocracy and played a prominent role both as a commercial enclave for cereal production and as a storage centre serving the *Emporion* area (Bouso et al., 2000; Fuertes et al., 2002).

The rural establishment was organised along a main axis, from which several domestic units have been identified. To date, three buildings with complex architecture (Houses 1 and 2, and House 3, which remains to be excavated) and two structures related to domestic and family use (Houses 8 and 10) have been documented (Colominas, 2008; Pons et al., 2010). An extensive silo field (Zone 20) was also associated with the settlement.

The anthracological analyses carried out at the site reveal the presence of mixed woodlands comprising holm oak (*Quercus ilex*) and sessile oak (*Quercus petraea*) in the vicinity of the rural establishment. Additionally, the occurrence of juniper (*Juniperus* sp.) and silver fir (*Abies alba*) has been documented. Moreover, the data attest to the existence of a riparian vegetation ecosystem (*Alnus* and *Ulmus*), typical of the marshy Empordà plain, rich in ponds and wetlands (Ros and Piqué, 2002).

Carpological data indicate a broad spectrum of crop varieties, encompassing both winter cereals, like wheat (*Triticum aestivum/durum)* and emmer (*Triticum dicoccum*), and spring types, such as millet (*Panicum miliaceum*), foxtail millet (*Setaria italica*), and oats (*Avena sativa*). Barley (*Hordeum vulgare*), which predominates along with millet, can be sown during both the spring and winter months. In the previous occupation phases of the settlement, its association with foxtail millet suggests that the two species were sown in conjunction during the spring. Furthermore, cereal production probably involved other intensive crop management strategies, such as biennial or triennial rotation systems (Alonso, 2000; Bouso et al., 2000; Canal, 2002). Finally, millet and foxtail millet are the only C_4 plants attested in the settlement.

The cultivation of cereal crops was integrated with legumes (Lens culinaris, *Pisum sativum*). The latter, although present in minor quantities in the establishment, are important not only for nitrogen fixation in the soil, maintaining a high level of fertility, but also for their high protein content. Vines and, to a lesser extent, olive trees are present among the fruits (Canal, 2000; Canal, 2002).

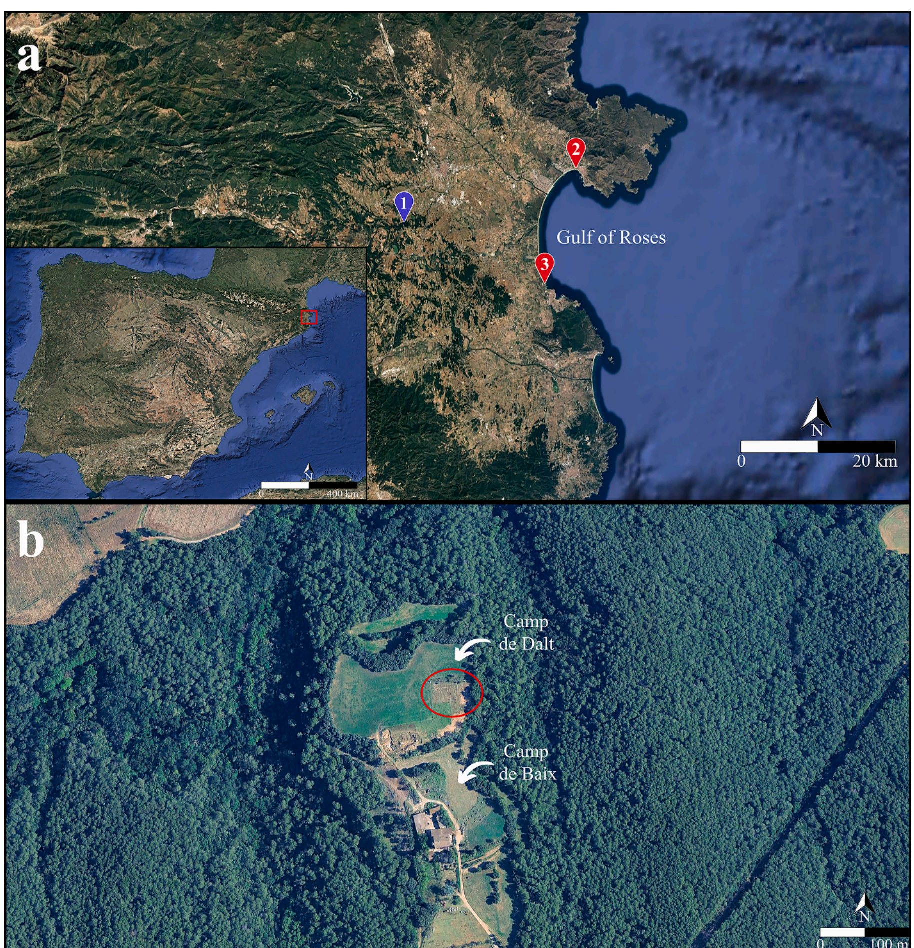

Fig. 1. **A**. Location of Mas Castellar de Pontós site (1) and the Greek colonies of *Rhode* (2) and *Emporion* (3) (Google Earth Pro modified); **b**. View of the archaeological complex stretching across the two hills: the upper one, known as "Camp de Dalt", and the lower one, identified as "Camp de Baix" (Google Earth Pro modified).

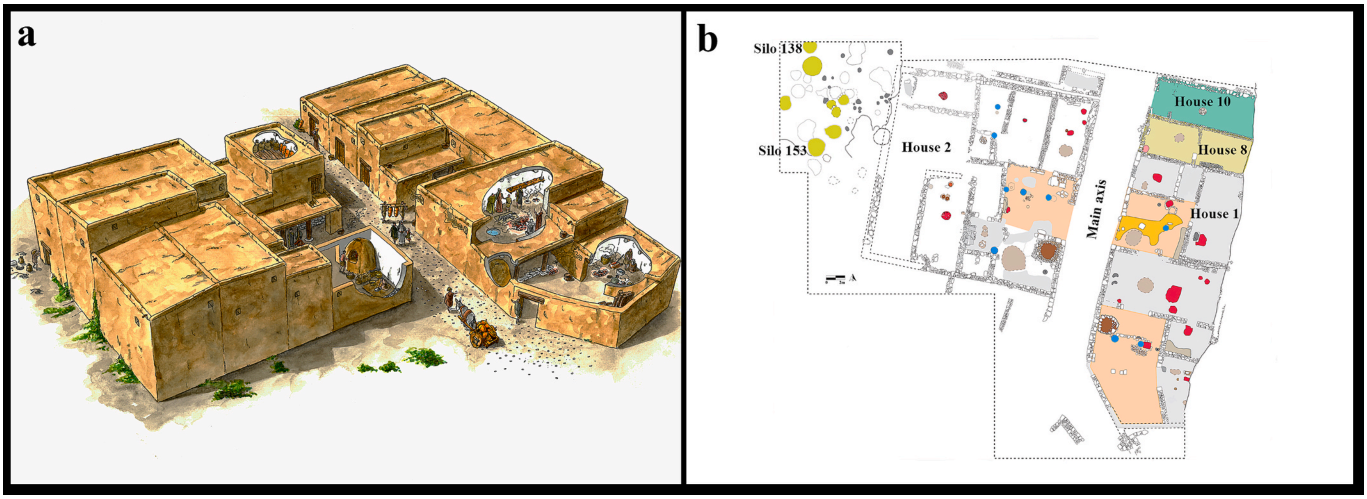

Fig. 2. **A**. Reproduction of the rural establishment (author Sergi Segura 2021) during Period V (250–180 BCE); **b**. Plan of the rural establishment (author Cristina Garcia-Dalmau 2010, modified); the teeth selected for this study come from House 2 and silos 138 and 153.

The archaeozoological study of the recovered faunal remains indicates a predominance of domestic species (99% of the recorded remains). Among these, caprines (*Ovis aries* and *Capra hircus*) are the most represented group (51%), with a predominance of sheep, followed by cattle (*Bos taurus*) and pigs (*Sus domesticus*). Hunting was an occasional activity with minimal impact on the diet (Colominas, 2013). However, the few remains of deer (*Cervus elaphus*), wild boar (*Sus scrofa*), and rabbits (*Oryctolagus cuniculus*) confirm the proximity of deciduous woodlands mixed with grasslands and pasture areas.

Finally, the recovery of sporadic remains of marine ichthyofauna, three bronze hooks and a net weight suggests that fishing was practised by the rural establishment community, even though it was a minority activity (Juan-Muns 2002). Moreover, the presence of malacological remains, especially bivalves (*Cerastoderma edule*, *Acanthocardia*), confirms direct contact between the coast and the inland area, mainly for commercial trading (Pons et al. 2002).

1.3. Husbandry strategies in the rural establishment

The MC community practised self-sufficient husbandry, breeding and rearing animals within the settlement, focused on obtaining diversified products from different species and adapting livestock strategies to the specific requirements of the settlement (Colominas, 2008, 2013; Messana, 2024).

The prevalence of adult and elderly sheep, alongside a bi-modulated reproduction pattern, with births occurring from winter to late spring and during autumn, suggests that secondary products, such as milk and wool, were exploited throughout the year (Colominas, 2008; Colominas, 2013; Messana et al., 2023). Sheep were mainly fed on C_3 plants; however, during the summer months, their isotopic carbon signature is enriched, suggesting the ingestion of C_4 plants in a minor proportion (Messana et al., 2025). Goats exhibit a similar pattern, with sacrifices mainly occurring in adulthood (Colominas, 2013), although information about their dietary and mobility patterns is still scarce.

Pigs were mainly slaughtered between 7 and 27 months of age and over 4 years old. This mortality profile is related to the exploitation of these animals for meat production, especially males at the optimum age and weight for slaughter, and the sacrifice of females once their reproductive capacity has been exhausted (Colominas, 2013).

Regarding cattle husbandry, the predominance of adult and old individuals suggests their primary exploitation as workforce in agricultural and/or transport activities (Colominas, 2008; Colominas, 2013; Colominas, 2017). Nevertheless, their exploitation for meat and milk production cannot be ruled out, since sacrifices at a juvenile age are also attested (Colominas, 2008; Colominas, 2013; Colominas, 2017). The bulk collagen analyses on cattle bone fragments performed by Messana and colleagues (2025), and the comparison with the isotopic data obtained for sheep, suggest a potential integration of C_4 plants into their diet (Supplementary Table S1 and Supplementary Fig. 1). However, the cattle's feeding habits remain poorly understood and undocumented on a seasonal level.

This study aimed to validate the integration of C_4 plants in the diet of cattle from Mas Castellar de Pontós and, eventually, to determine the timing and duration of their consumption, through the sequential analysis of dental enamel. Establishing the seasonality of C_4 intake is critical for evaluating whether these resources reflect deliberate foddering practices, exploitation of diversified plant resources, or opportunistic responses to seasonal environmental constraints. Furthermore, the research sought to identify the nature of the C_4 plants consumed to better understand livestock management strategies and the relationship between the settlement's population and the surrounding landscape during the Late Iron Age.

1.4. Stable isotopes and herding feeding habits

Investigating the feeding habits of past herds is essential for reconstructing their breeding, maintenance, and exploitation. Traditionally, the environmental characteristics of the territories available for grazing have been determinant for the livestock feeding strategies employed by herders. Furthermore, animal feeding frequently follows a seasonal pattern, shaped by pasture availability or shifting between complementary areas, as grass represents the least labour-intensive and most cost-effective nutrient source (Andugar and Saña, 2004; Walsh et al., 2023). Nevertheless, herders could employ alternative strategies to feed the livestock. One alternative involves the exploitation of forests and less productive lands, where the herds would consume leaves and fine branches (Halstead, 1996). Another option is the integration with the agricultural calendar, introducing cereals into the livestock diet in the form of fodder or forage to supplement seasonal shortages in pasture. Moreover, agricultural by-products – such as pruned leaves and bark, almonds, olives, vines, walnuts, or fig trees – could also be used as fodder (Forbers, 1998). Hay is another example of fodder, involving the storage and drying of the selected plants to maintain their nutritional value (Lavin et al., 1993). These different feeding strategies can be combined or employed independently. Each of them entails distinct labour requirements for herders and implies differing degrees of social organisation and environmental exploitation within the community.

Stable isotope analysis is nowadays a reliable and widely adopted tool for reconstructing individuals' past diets by measuring the biochemical composition of preserved body tissues in the archaeological record. The isotopic signatures of food and water ingested by an animal are recorded in its teeth and bones. In the case of teeth, enamel does not remodel once mineralised and reflects the isotopic signal recorded during its formation. In cattle, the crown formation of the second molar (M_2) begins between the first and second month of life and is completed at around 12 months. On the other hand, the third molar (M_3) begins to form from the tenth month onwards and is completed at around two years of age (Brown et al., 1960). Therefore, each of the two molars analysed individually provides a record of one year of an individual's life; combined, they trace back the first two years of a cattle's life. Thus, the sequential carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) analysis of dental enamel provides an insight into an individual's feeding behaviour and pasture environment during the period of tooth formation.

The $\delta^{13}C$ isotopic values measured in the dental enamel mineral fraction (i.e. bioapatite compound) reflect the carbon isotopic composition of the plants consumed by an individual (Lee-Thorp and Van der Merwe, 1987). This varies in accordance with the photosynthetic pathways of the plants, i.e. C_3 and C_4 (Bender, 1971; Farquhar et al., 1989). The average $\delta^{13}C$ value for C_3 plants is −28.5‰, with a range from −20‰ to −37‰ and a recommended maximum threshold of −23‰ for typical C_3 species. On the other hand, C_4 plants display an average $\delta^{13}C$ value of −13‰, ranging from −10‰ to −14‰. Extremely low $\delta^{13}C$ values are indicative of the exclusive consumption of plants grown within dense, closed-canopy forests, with a cut-off of −31.5‰ (Tieszen and Boutton, 1989; Tieszen, 1991; Kohn and Cerling, 2002; Kohn, 2010). These values have been calculated in modern plants, whereas for pre-industrial vegetation, a correction factor of + 1.5‰ is required to compensate for the fossil fuel effect, resulting in an effective upper threshold of −21.5‰ for C_3 plants (Friedli et al., 1986; Marino and McElroy, 1991; Feranec and MacFadden, 2006). Moreover, large ruminant mammals display an isotopic enrichment factor (ε^*) of 14.1 ± 0.5‰ between consumed plants and enamel bioapatite $\delta^{13}C$ values (Cerling and Harris, 1999). In the present study, dietary $\delta^{13}C$ values exceeding −21.5‰ and corresponding to approximately −7.7‰ in the dental enamel of the individuals analysed, are indicative of a transitional zone reflecting an increasing probability of C_4 plants intake (Fabre et al., 2023). Wild C_4 plants are either non-existent or residual in the temperate environments of western Europe (Mateu, 1992; Pyankov et al., 2010). Nevertheless, a small portion of wild C_4 plants, particularly halophytic communities, is attested in the coastal marshes area of the Empordà plain, especially in the Gulf of Roses (Houérou, 1994; Gesti, 2006; Casals, 2007; Ejarque et al., 2016).

The $\delta^{18}O$ isotopic values recorded in bioapatite are primarily derived from ingested water and consumed plants (Longinelli, 1984; Luz et al., 1984). These isotopic signatures are related to meteoric water and temperature, both of which fluctuate seasonally at temperate latitudes. Consequently, at mid and high latitudes, higher $\delta^{18}O$ values correspond to the warm season, whilst lower $\delta^{18}O$ values are indicative of the cold season (Gat, 1980). Therefore, the combination of $\delta^{13}C$ and $\delta^{18}O$ sequences along the tooth crown enables the characterisation of an individual's diet during the first years of life with a seasonal resolution.

2. Materials and Methods

2.1. Materials: Tooth enamel samples

Sequential carbon ($\delta^{13}C_{enamel}$) and oxygen ($\delta^{18}O_{enamel}$) isotope analyses were conducted on seven lower molars (four second molars and three third molars), relatively dated between 250 and 180 BCE, and belonging to five cattle. For two of these individuals, both second and third molars were sampled. All the selected teeth exhibit either completely or almost fully formed crowns, as well as early wear stages. Table 1 provides descriptive information (side, wear stage, estimated age of death, and provenience) about the molars selected for this study.

Three of the second molars belong to the Grant's (1982) wear stage K (4–6.5 years) and one to the wear stage G (~2 years), whilst two third molars belong to the wear stage H (2–4 years) and one to the wear stage K (4–6.5 years). Four teeth were found in House 2 of the rural establishment, while three molars were discovered inside two pits (silos 138 and 153) associated with the house.

2.2. Methods: Sequential carbon and oxygen isotope analysis

The surface of the selected teeth was cleaned by abrasion using a tungsten drill. Enamel bands were then sequentially sampled with a diamond drill. Sampling was conducted on the buccal surface, specifically on the distal lobe of the M_2 and the central lobe of the M_3 in cattle remains. Samples were collected at 1–2 mm intervals from the apex to the enamel–root junction (ERJ) of each tooth. The positions of the sampled bands were recorded in millimetres along the entire crown, commencing from the ERJ. Both drilling and subsequent chemical treatment of the samples were performed at the READ Laboratory of the Autonomous University of Barcelona (UAB).

A total of 147 enamel powder samples (ranging from 13 to 31 samples per tooth) were collected from cattle molars, weighing between 2.9 and 8.5 mg. Following the protocol described by Balasse et al. (2002) and modified by Tornero et al. (2013), the bioapatite samples were treated to eliminate exogenous carbonate contamination (4 h in 0.1 M acetic acid [CH_3COOH]; 0.1 ml solution per mg of sample), subsequently rinsed several times with distilled water, and dried in an oven at 70°C for 48 h. The treated samples were then measured using an automated carbonate preparation device (KIEL-III) coupled to a Finnigan MAT 252 isotope ratio mass spectrometer (IRMS) at the Environmental Isotope Laboratory, Department of Geosciences, University of Arizona (USA).

Powdered enamel samples were reacted with dehydrated phosphoric acid under vacuum at 70°C. To ensure analytical accuracy and precision, the international standards NBS-19 and NBS-18 were employed. The mean analytical precision, determined from replicate measurements of standards within each analytical run, was ± 0.1‰ for $\delta^{18}O_{enamel}$ and ± 0.08‰ for $\delta^{13}C_{enamel}$ (1σ). The isotope composition is expressed in δ notation, reported in per mil (‰), and normalised to the Vienna Pee Dee Belemnite (V-PDB) standard for both carbon and oxygen values.

3. Results

Results of the intra-tooth sequences of $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$

Table 1
Cattle tooth specimens (ID) sampled for the sequential carbon and oxygen analyses in this study: side (L, left; R, right), wear stages and estimated age at death according to Grant (1982), and provanance; na, no analysed.

Teeth ID	Side	M_2		M_3		Provenance
		Wear stage	Age estimation	Wear stage	Age estimation	
MC 11144	R	K	4–6.5 years	na	na	House 2
MC 11147	L	K	4–6.5 years	na	na	House 2
MC 12028	R	G	≃ 2 years	H	2–4 years	House 2
MC 20129	L	K	4–6.5 years	K	4–6.5 years	Silo 138
MC 20165	R	na	na	H	2–4 years	Silo 153
*Grant 1992						

values from cattle's molars are summarised in Table 2 and fully presented in Fig. 3 and Supplementary Table S2. The $\delta^{13}C_{enamel}$ values from all samples range from −4.8‰ to −11.7‰, with a mean of −9 ± 1.8‰ (SD). The mean $\delta^{13}C_{enamel}$ values within specimens range from −7.4‰ to −10.7‰, with maximum values varying between −4.8‰ and −10.1‰, and minimum values between −9.4‰ and −11.7‰. The $\delta^{18}O_{enamel}$ values across all samples range from 0.4‰ to −3.4‰, with an overall mean of −1.6 ± 1‰ (SD). Within each specimen, the mean $\delta^{18}O_{enamel}$ values range from –0.5‰ to −2.2‰, maximum values from 0.4‰ to −1.4‰, and minimum values from −1.5‰ to −3.4‰.

Both the $\delta^{18}O_{enamel}$ and $\delta^{13}C_{enamel}$ sequences of almost all cattle from the rural establishment exhibit relatively large intra-tooth variation, with a sinusoidal pattern and clear maximum and minimum events, reflecting the seasonal cycle. The second molars of cattle MC 11144 and MC 11147 constitute exceptions to this pattern, as they display no definite maximum or minimum events. However, seasonal variation is evident within their sequences.

Although all the individuals analysed exhibit $\delta^{13}C_{enamel}$ values consistent with a diet primarily based on C_3 plants, most of the cattle (MC 11147, MC 12028, and MC 20165) display $\delta^{13}C_{enamel}$ values higher than −7.7‰ along the sequence, coinciding with the descending $\delta^{18}O_{enamel}$ values that follow the maximum peak along the tooth enamel crown (Fig. 3).

4. Discussion

Livestock feeding management.

The data obtained from the sequential analysis of cattle dental enamel provided further insight into the seasonal feeding strategies of livestock adopted by the Iberian community of Mas Castellar de Pontós during the Late Iron Age. The results reveal that at the rural establishment, cattle feeding strategies included the occasional contribution of C_4 plants to the fodder during the warm season (i.e. during summer and early autumn), when grazing resources were potentially limited. Indeed, the carbon sequences from the cattle's molars from MC display a large amplitude and closely mirror the fluctuations of the oxygen sequences, indicative of seasonal changes. These variations are consistent with a feeding regime influenced by seasonal climate variability and the resulting availability of plant resources throughout the year. Specifically, the data indicate that cattle from the rural establishment primarily consumed C_3 plants. Indeed, the five individuals analysed exhibit $\delta^{13}C_{enamel}$ values predominantly lower than −7.7‰ and, consequently, falling within the expected range for C_3-type species (Fig. 3 and Supplementary Table S2). Nevertheless, three out of six individuals (MC 11147, MC 12028, and MC 20165) display seasonal variability in the carbon values. Indeed, along the tooth crown, these individuals exhibit $\delta^{13}C_{enamel}$ values exceeding the transition zone defined for mixed C_3/C_4 intake, indicating the consumption of C_4 plants in concomitance with the decreasing $\delta^{18}O_{enamel}$ values recorded immediately after the summer peak. This suggests a contribution of C_4 plants during specific and brief periods of the year, most likely during summer and autumn seasons, rather than throughout the year. Regarding the two remaining individuals, the second molar of cattle MC 11144 exhibits a progressive increase in $\delta^{13}C_{enamel}$ values towards the end of the crown, recorded at the end of the summer. The absence of the third molar makes it impossible to verify whether this upward trend continued beyond the transitional zone at which $\delta^{13}C_{enamel}$ values indicate a dietary contribution of C_4 plants. Finally, the second molar of individual MC 20129 exhibits $\delta^{13}C_{enamel}$ values consistent with an exclusively C_3 plant-based diet. However, the third molar of the same individual shows a progressive increase in $\delta^{13}C_{enamel}$ values recorded towards the end of the crown, during the warm season, which may suggest the consumption of C_4 plants. Moreover, if these two individuals had consumed C_4 plants in a lower proportion, the analytical approach employed would not allow us to detect or confirm their presence in the diet.

A similar behaviour, characterised by seasonal consumption of C_4 plants, was observed in sheep from the same settlement. Indeed, the eight individuals previously analysed in Messana et al., 2025 exhibited $\delta^{13}C_{enamel}$ values indicative of a diet predominantly based on C_3 plants (Fig. 4 and Supplementary Table S3). Nonetheless, three individuals – MC 11144, MC 20102, and MC 20160 – display a different pattern. The $\delta^{13}C_{enamel}$ sequence from the M_2 of individual MC 11144 shows values close to the transition zone established around −7.7‰, suggesting that C_4 plants could have contributed to its diet during its second summer of life. However, due to the crown wear, no information is available for its first summer alive, making it uncertain whether this C_4 input represents a recurrent seasonal practice or a punctual event. In the cases of individuals MC 20102 and MC 20160, there is evidence of a contribution of C_4 plants to their diet during their first summer. Indeed, the $\delta^{13}C_{enamel}$ values exceed the transition zone defined for the mixed contribution of C_3/C_4 plants in concomitance with the peak of $\delta^{18}O_{enamel}$ values. For individual MC 20160, it was also possible to analyse its M_3, revealing a $\delta^{13}C$ sequence with reduced amplitude and values consistent with a C_3 plant-based diet ($\delta^{13}C_{enamel}$ values ranging from −10.7‰ to −13.4‰, with a mean of −11.7 ± 0.8‰ SD). Therefore, these results suggest that the incorporation of C_4 plants in the diet of individual MC 20160 occurred on a punctual seasonal basis. Overall, the data indicate that at Mas Castellar de Pontós, the feeding strategies for both cattle and sheep included the occasional seasonal consumption of C_4 plants when C_3 grazing resources (especially herbaceous plants) were potentially limited in the landscape (i.e. during the warmer months).

The data obtained from bulk collagen analyses performed on cattle bone remains are consistent with a limited consumption of C_4 plants at specific times in the individuals' lives (Messana et al., 2025; supplementary Table S1 and Supplementary Fig. 1). Indeed, the $\delta^{13}C_{collagen}$ values are not sufficiently enriched to support a sustained consumption of C_4 plants. Cattle MC 12028 displays $\delta^{13}C_{enamel}$ values ranging from −9.9‰ to −5.1‰, indicating the integration of C_4 plants in its diet. The $\delta^{13}C_{collagen}$ value measured in a mandible fragment from the same individual is −19.2‰. While this value is slightly enriched relative to the average expected for strictly C_3-based diets in temperate pre-industrial environments, it does not in itself constitute unequivocal evidence of substantial C_4 intake. Rather, it could reflect an attenuated signal of limited or seasonal C_4 consumption, consistent with the enamel sequence. The $\delta^{15}N_{collagen}$ value is 6.1‰, accordant with the grazing nature of the species. Individual MC 20129 provided similar $\delta^{13}C_{collagen}$

Table 2
Summarised $\delta^{18}O_{V\text{-}PDB‰}$ and $\delta^{13}C_{V\text{-}PDB‰}$ values measured on enamel samples from the lower second (M_2) and third (M_3) molars of cattle from MC: mean, range, maximum (max.), and minimum (min.) isotopic values.

Taxon	Teeth	Sample	*n*	$\delta^{18}O_{V\text{-}PDB‰}$ Mean	Range	Max.	Min.	$\delta^{13}C_{V\text{-}PDB‰}$ Mean	Range	Max.	Min.
Bos taurus	M_2	MC 11144	13	−2.0	1.3	−1.4	−2.7	−9.9	2.6	−8.4	−11.0
		MC 11147	15	−1.5	2.4	0.0	−2.4	−8.7	4.0	−7.0	−11.0
		MC 12028	25	−1.4	2.7	−0.2	−2.9	−7.7	4.8	−5.1	−9.9
		MC 20129	18	−0.5	1.9	0.4	−1.5	−10.7	1.6	−10.0	−11.7
	M_3	MC 12028	31	−1.4	3.8	0.8	−3.0	−7.4	4.6	−4.8	−9.4
		MC 20129	22	−2.2	2.6	−0.7	−3.4	−10.5	3.5	−8.0	−11.5
		MC 20165	23	−2.0	2.5	−0.7	−3.3	−9.8	4.1	−7.6	−11.7

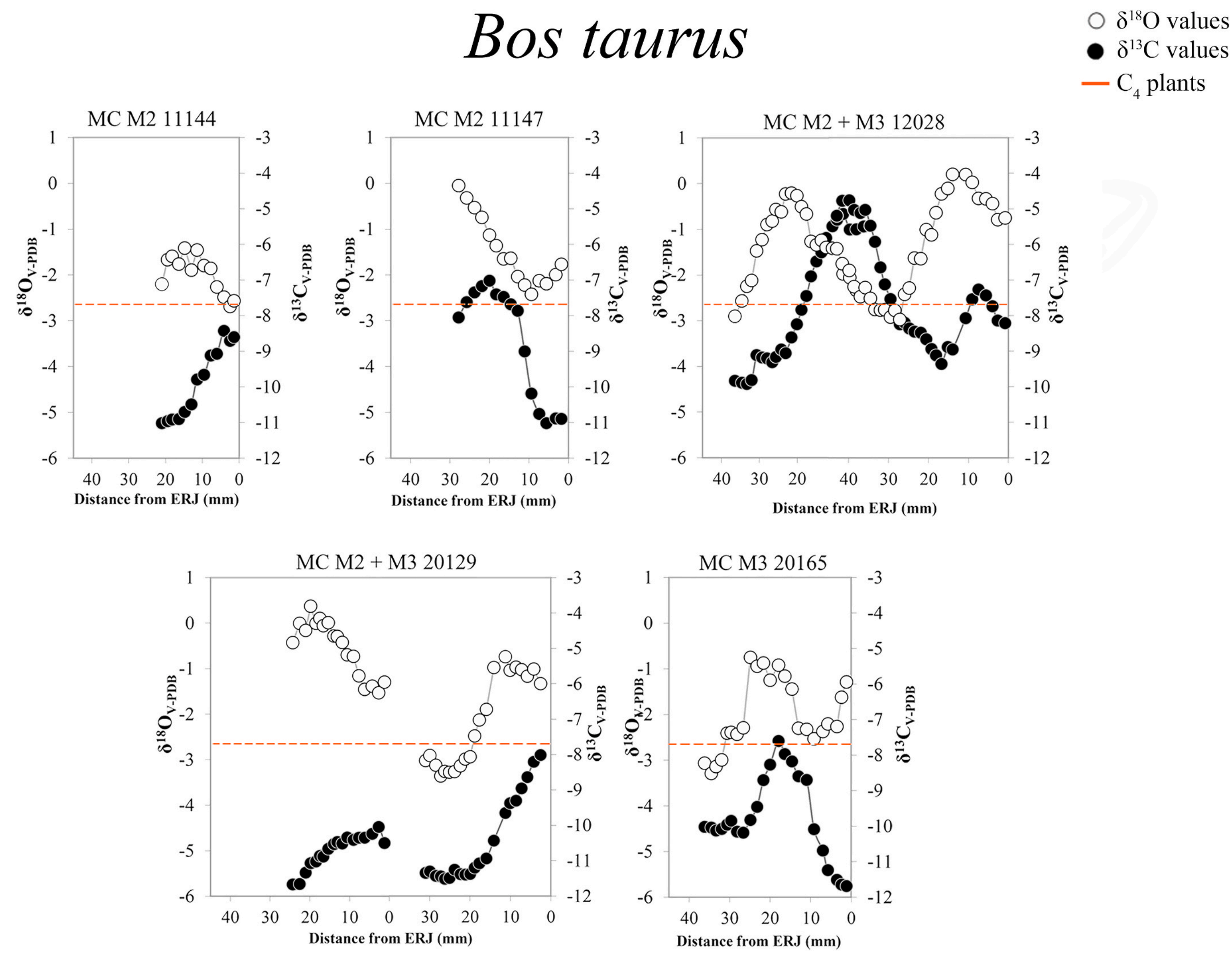

Fig. 3. $\delta^{18}O_{V\text{-}PDB‰}$ (white dots) and $\delta^{13}C_{V\text{-}PDB‰}$ (black dots) sequences measured on the dental enamel of the M_2 and M_3 of selected cattle from the rural establishment. The M_2 and M_3 of the same individuals (MC 12028 and MC 20129) are presented together. The dashed orange line indicates the threshold of −7.7‰ beyond which $\delta^{13}C_{enamel}$ values are interpreted as indicative of a dietary contribution from C_4 plants.

(−19.2‰) and $\delta^{15}N_{collagen}$ values (6.2‰), which could therefore suggest a minor intake of C_4 plants, as further hypothesised by the progressive increase in $\delta^{13}C_{enamel}$ values recorded in the third molar of the same individual. A fragment of cattle radius, belonging to an individual aged between two and four years old and recovered from silo 153, exhibits a lower $\delta^{13}C_{collagen}$ value than the two previous individuals (−20.2‰) and a slightly higher $\delta^{15}N_{collagen}$ value (7.0‰) in comparison with the majority of the other individuals. Given its comparable age and provenance – both from the same silo and stratigraphic unit – as cattle specimen MC 20165, whose third molar was analysed, it is highly probable that these remains correspond to the same individual. Sequential analysis of the tooth enamel had revealed a slight intake of C_4 plants during the warm season, which is not reflected in the carbon isotopic composition of the bone fragment. However, the $\delta^{15}N_{collagen}$ value could indicate the consumption of plants grown in ^{15}N-enriched soils. Individual MC 20158 also displays a higher $\delta^{15}N_{collagen}$ value (7.3‰), concomitant with a $\delta^{13}C_{collagen}$ value which may reflect sporadic consumption of C_4 plants (−19.4‰). The remaining six individuals analysed show $\delta^{15}N_{collagen}$ values ranging from 5.2‰ to 6.5‰, consistent with diets based on plants grown in soils not enriched in ^{15}N. Among these, individuals MC 11125, MC 11150, MC 20168, and MC 100030 exhibit $\delta^{13}C_{collagen}$ values between −18.3‰ and −19.2‰, suggesting possible consumption of C_4 plants at some point in their lives.

The integration of C_4 plants in the livestock's diet from MC is also attested by data obtained from sequential and bulk collagen analyses carried out on sheep remains and published in Messana et al., 2025 (Fig. 4, Supplementary Table S1, and Supplementary Table S3). Therefore, cattle and sheep from the rural settlement had a diet primarily based on the consumption of C_3 plants, with seasonal integration of C_4 plants during the warmer season in some individuals. In the case of cattle, even higher carbon values are recorded than in sheep, indicating a greater incorporation of C_4 plants into their diet or over a longer period. Furthermore, some individuals of both species consumed plants potentially growing in ^{15}N-enriched soils.

As previously reported (see Sect. 1.1), the presence of wild C_4 plants is attested in the coastal marshes of the Empordà plain, especially in the Gulf of Roses, and may have represented a food resource for livestock (Houérou, 1994; Gesti, 2006; Casals, 2007; Ejarque et al., 2016). Indeed, this area is characterised by a marshland flora consisting of marsh samphire, meadows, and halophytic rushes and shrubs such as *Atriplex halimus* (Folch & Guillén 1981; Hereu Fina et al. 2012). The use of wild halophytes as livestock feed is well documented in the Mediterranean basin. Although the high salt content and various anti-nutritional factors inherent in these plants, their digestibility and nutritional value are enhanced when consumed in mixed feeds (Houérou, 1994; El Shaer and Attia-Ismail, 2002; El Shaer, 2006; Stringi et al., 2009; Walker et al.,

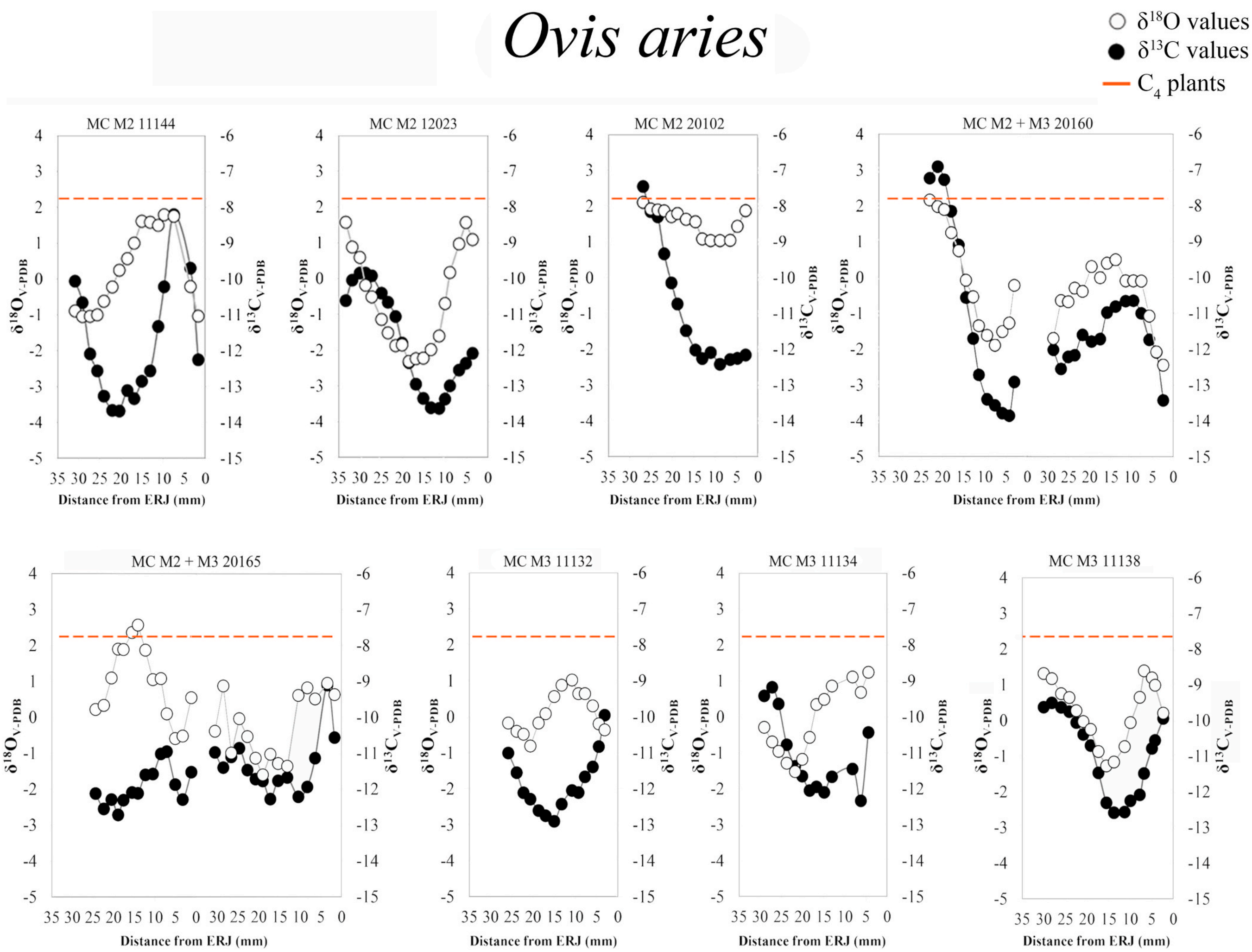

Fig. 4. $\delta^{18}O_{V\text{-}PDB‰}$ (white dots) and $\delta^{13}C_{V\text{-}PDB‰}$ (black dots) sequences measured on the dental enamel of the M_2 and M_3 of selected sheep from the rural establishment. The M_2 and M_3 of the same individuals (MC 20160 and MC 20165) are presented together. The dashed orange line indicates the threshold of −7.7‰ beyond which $\delta^{13}C_{enamel}$ values are interpreted as indicative of a dietary contribution from C_4 plants. The isotopic values for sheep have previously been published in Messana et al. (2025).

2014; Abd El-Hack et al., 2018; Hasnain et al., 2023). Furthermore, opportunistic consumption of marine vegetation, such as seaweed and seagrasses, during drought conditions in warmer seasons cannot be completely ruled out. Indeed, in coastal areas, seaweed is a valuable alternative feed for livestock and a source of highly valuable nutrients, minerals, and proteins (Evans and Critchley, 2014; Rey-Crespo et al., 2014; Makkar et al., 2016). Marine macrophytes typically display elevated $\delta^{13}C$ values (Hemminga and Mateo, 1996; Raven et al., 2002; Blanz et al., 2020). Consequently, their short-term contribution to the livestock diet from the rural settlement would be consistent with the seasonal $\delta^{13}C_{enamel}$ enrichments documented in the sequential records. Seaweed has long been used as livestock fodder, with references dating back to ancient Greece and Icelandic sagas (Evans and Critchley, 2014; Makkar et al., 2016). In coastal North-western Europe, marine seaweed has been traditionally grazed or fed to sheep, horses, and cattle during periods of fodder scarcity. During the 19th century and early 20th century, numerous cases of occasional or systematic use of seaweed for livestock feeding were documented in France (Brittany), the Scottish islands, and Scandinavia (Amorosi et al., 1998; Evans and Critchley, 2014; Makkar et al., 2016). Furthermore, sequential carbon isotope analyses on sheep teeth from the Orkney Islands in Scotland provided the first archaeological evidence of seaweed consumption by sheep during the Neolithic period (Balasse et al., 2006, 2019). However, in contrast to North-western Europe, there is no well-documented tradition of Mediterranean livestock grazing seaweed in pastoral systems, particularly during the warmer seasons.

If the elevated carbon values observed in the livestock from the rural establishment derived from the consumption of wild C_4 plants and/or marine vegetation, part of the cattle herd and sheep flock would have seasonal access to different grazing areas: C_3 grasslands near the settlement during the cooler months, and coastal marshlands during the warmer seasons. Economic contacts between the rural establishment community and the coastal area are well attested by the evidence of imported products and transport amphorae, as well as by the remains of marine ichthyofauna and bivalve molluscs, in addition to the presence of fishing tools in the settlement (Bouso et al., 2002; Juan-Muns 2002; Pons et al. 2002, 2010). Therefore, it cannot be ruled out that livestock movements towards the coastal area were also part of these interactions.

Navarrete and colleagues (2025) provide additional isotopic evidence for the consumption of wild C_4 plants by cattle in the eastern Iberian Peninsula. Indeed, at the Neolithic sites of Mas d'Is and Niuet (Serpis Valley), the authors recorded $\delta^{13}C_{collagen}$ values in cattle bone remains consistent with the intake of C_4 plants grown in the wetlands and marshes of the Serpis Valley. Moreover, the $\delta^{13}C_{collagen}$ values of a limited number of cattle from the surrounding Neolithic sites of La Vital and Costamar could indicate their access to flood zones (Salazar-García, 2009, 2011; Navarrete et al., 2025).

Regarding later periods, the study by Gallego et al. (2017) investigated the diet of ninety-nine sheep from three Roman settlements in the Empordà plain – Empúries, Mas Gusó, and Tolegassos – using the dental microwear technique. The results, relative to the last meals consumed, indicate a diet consisting primarily of leaves and tender plants, with a predominantly grazing behaviour of the sheep. By integrating these results with palaeoenvironmental data, the authors suggest that Empordà communities moved their flocks to pasture in the wetlands and marshes of the coastal areas, thus avoiding conflict with cultivated land. This herd management documented in the Republican Empordà is fully consistent with Cato's strategy of investing in marshland to obtain highly profitable pastures (Colominas and Olesti, 2025). Moreover, classical sources provide indirect evidence for livestock grazing in coastal or estuarine environments: Strabo (3.2.4) mentions cattle grazing in the estuaries of Baetica, despite the danger posed by the advancing tide, and Martial refers to the river Betis as the one “that feeds the Iberian herds” (Marziale MV Epigrammaton). Therefore, the results of our study may not only support the possibility that the seasonal exploitation of wetland or coastal environments for livestock grazing formed part of broader pastoral practices in the Iberian Peninsula but also constitute the first evidence of its occurrence in this area.

As an alternative hypothesis, the incorporation of C_4 plants into the diets of cattle and sheep at Mas Castellar de Pontós may suggest the supplementation of their forage with cultivated cereals. The cultivation of C_4 cereals such as millet and foxtail millet at the rural establishment could support the plausibility of their use as seasonal fodder. In this way, the presence of both winter and spring crops within the settlement would have guaranteed the availability of crop residues for a significant portion of the year, particularly during seasonal periods when grazing resources were limited (Canal, 2000; Canal, 2002). In Book VI of his Latin treatise *De re rustica*, Columella refers to the use of cereal chaff for cattle feed, identifying millet as the most common option, followed by barley and wheat (VI.III.3). Moreover, the possible use of cattle and sheep for field clearance between sowing seasons cannot be excluded. In the case of cattle, access to cultivated fields and the consumption of C_4 cereals could have been a result of their employment as a labour force in agricultural activities. Although the limited number of pathologies observed in cattle remains is not related to animal overexertion, the recovery of five ploughshares from the settlement would suggest their use for traction purposes (Rovira 2002; Colominas, 2013). Finally, seasonal variations in feeding habits may also reflect forage supplementation provided to pregnant females or to males preparing for mating.

The presence of individuals with slightly higher $\delta^{15}N_{collagen}$ values among both cattle and sheep indicates that these animals have been grazing on ^{15}N-enriched soils. These data could support either the hypothesis of C_4 cereals consumption from manured fields or the intake of halophyte plants and/or marine vegetation from coastal salt marshes. Indeed, both cereals cultivated on fertilised fields and wild plants growing along coastlines and in salt marshes are significantly enriched in ^{15}N compared to other terrestrial plants (Bogaard et al., 2007; Britton et al., 2008).

Based on the isotopic data currently available, it is not possible to ascertain which of the two scenarios outlined above represents the feeding strategy adopted for the livestock from the rural establishment. The inability to discriminate between the two hypotheses is a clear example of equifinality, a concept defined by von Bertalanffy (1968), according to which “the same final state may be reached from different initial conditions and in different ways”. Further analyses integrating the current data are required to enhance our understanding of the livestock feeding strategies employed by the MC community and to provide deeper insight into the complex husbandry system within the settlement.

Despite the inability to ascertain the nature of the C_4 plants seasonally consumed by part of the livestock from the rural establishment, whether wild species or cultivated cereals, the observed variability in the $\delta^{13}C$ values of certain individuals indicates the ingestion of plants with different isotopic compositions. The access by livestock to a broader range of plant resources may reflect deliberate foddering practices, seasonal shifts in resource availability, differential access to grazing areas, or opportunistic exploitation of marginal resources. The adoption of seasonal feeding strategies suggests that the MC community aimed not only to meet the specific requirements of each animal, but also to maximise the use of available food resources, whether these were cultivated cereals or wild plants.

A comparable pattern is attested in the contemporary settlement of Turó de la Rovira, situated in the Barcelona plain, on top of a small promontory near the Mediterranean coast. Here, the results from bone collagen and sequential dental analyses suggest an integration of C_4 plants, probably on a seasonal basis, into the diet of sheep and cattle. As in the case of MC, livestock may have consumed either cultivated cereals or wild plants from coastal salt marshes (Messana et al., 2025). Therefore, these data suggest that Iberian herders during the Late Iron Age supplemented their livestock's diet with C_4 plants according to necessity. At the Can Roqueta site (Barcelona), dated between the late Bronze Age and early Iron Age (1300 and 550 cal. BC), Albizuri and colleagues (2021) documented the intake of C_4 cereals, specifically millet, by cattle and horses. Furthermore, the authors also attested to the consumption of C_4 cereals by dogs and foxes, suggesting a commensal relationship with humans. Along these lines, three dog remains from the rural establishment of MC display elevated $\delta^{13}C_{collagen}$ values (−16.97‰, −17.50‰, and −18.25‰; Messana et al., 2025), suggesting the consumption of C_4 plants. Again, this could be due to the inclusion of millet into their dietary regimen, following adaptation to the dietary habits of their masters. These data could provide further support for the hypothesis of C_4 cereal intake by cattle and sheep, rather than the integration of wild C_4 plants growing in coastal marshlands.

5. Conclusion

The results of this research support the hypothesis previously proposed by Messana et al. (2025) that C_4 plants contributed seasonally to the cattle diet at Mas Castellar de Pontós. Indeed, sequential analysis performed on dental enamel provided a more comprehensive understanding of the feeding habits of the cattle from the rural establishment, expanding the existing data obtained from the bulk collagen analysis on bone remains. The sequential analysis of $\delta^{18}O_{enamel}$ and $\delta^{13}C_{enamel}$ allowed the reconstruction of the cattle's feeding habits during approximately their first two years of life, with seasonal resolution. This level of detail was inevitably forfeited through the bulk analysis of bone collagen.

The data reveal, for the first time, the cattle feeding strategies adopted seasonally by one of the most complex Iron Age communities in the northeastern Iberian Peninsula. This aspect is essential for understanding not only the management and exploitation of livestock, but also the interaction between the community and the surrounding landscape. Cattle and sheep from the rural settlement had access to a diversified range of plant resources in different times of the year: feeding on C_3 plants during the colder months and supplementing with C_4 plants during the warmer seasons. The adoption of seasonal livestock feeding strategies suggests that the community aimed not only to meet the specific requirements of each animal, but also to maximise the availability of pasture and/or fodder. The presence of isotopic signals indicating C_4 plant contribution in only some cattle and sheep could reflect herders' adoption of individualised feeding strategies. These could involve access to cultivated fields for clearing between sowing seasons for only part of the herd, or the supplementation of fodder provided to specific individuals, such as pregnant or lactating females and males preparing for mating. However, a uniform management of the entire herd cannot be ruled out, in which case a minor intake of C_4 plants by certain individuals would not be detectable through the analytical approach employed in our studies.

Two main scenarios are plausible: seasonal access to wild C_4 halophytic communities and marine vegetation in nearby coastal environments, or the integration of cultivated C_4 cereals into animal fodder. If the seasonal integration of C_4 plants into the livestock diet involved the consumption of cultivated cereals, such as millet or foxtail millet, then it is plausible that within the settlement, agricultural and husbandry practices were closely intertwined and perfectly integrated within the settlement's productive schedule. On the other hand, if the livestock's feeding habits included wild plants growing along the coast and in salt marshes, the rural settlement community would likely have benefited from contacts with the coastal regions to extend the accessible pasture areas. In either case, both scenarios are consistent with flexible livestock management practices and reinforce the idea that animal husbandry played a significant role in the site's economy during the Late Iron Age.

Finally, the results once again demonstrate the crucial importance of integrating different biogeochemical analyses with zooarchaeological data to achieve a more comprehensive picture of livestock feeding habits and, consequently, of the economic and social dynamics within protohistoric societies.

CRediT authorship contribution statement

Messana Chiara: Writing – original draft, Methodology, Investigation. **Tornero Carlos:** Writing – review & editing, Validation, Supervision, Funding acquisition. **Pons Enriqueta:** Writing – review & editing, Validation. **Colominas Lídia:** Writing – review & editing, Validation, Supervision, Funding acquisition.

Funding

Sequential carbon analyses for this study received financial support from the project "*Seasonal feeding habits of cattle over time: the case of Mas Castellar de Pontós (Girona, Spain). Fundación Palarq, convocatòria Palarq Analíticas 2024/2025*". C.M.'s work is supported by the READ project, funded by the European Research Council (ERC) under the European Union's HORIZON ERC programme (Grant agreement No. 101088071; led by CT). The Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA) has received financial support from the Spanish Ministry of Science and Innovation through the "*María de Maeztu*" program for Units of Excellence (CEX2024-01485-M/ funded by MICIU/AEI). CT's work was supported by the Spanish Ministry of Science and Innovation (RYC 2020–029404-I). LC's work was supported by the Spanish Ministry of Science and Innovation (RYC 2019–026732-I).

Author Contributions.

C.M. selected, sampled, and prepared the dental remains for isotope analysis, wrote the main manuscript, prepared figures, processed and interpreted the data. C.T., L.C., and E.P. contributed to the data interpretation and reviewed the manuscript. All the authors approved the submitted version.

Data availability.

All data generated or analysed during this study are included in this published article (and its supplementary information files).

Code availability.

Not applicable.

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.

Acknowledgements

The authors thank Dr David Dettman and Todd Lange for the scientific supervision on the IRMS data, and the anonymous reviewers for their valuable feedback and comments, which have served to strengthen the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2026.105704.

References

Abd El-Hack, M.E., Samak, D.H., Noreldin, A.E., Arif, M., Yaqoob, H.S., Swelum, A.A., 2018. Towards saving freshwater: halophytes as unconventional feedstuffs in livestock feed: a review. Environ. Sci. Pollut. Res. 25, 14397–14406. https://doi.org/10.1007/s11356-018-2052-9.

Adroher A, Pons E (2002) Els treballs arqueològics. In: Pons E (ed) Mas Castellar de Pontós (Alt Empordà). Un complex arqueològic d'època ibèrica (Excavacions 1990-1998). Girona, Sèrie Monogràfica 21. Museu d'Arqueologia de Catalunya, pp. 17-33.

Albizuri, S., Grandal-d'Anglade, A., Maroto, J., Oliva, M., Rodríguez, A., Terrats, N., Palomo, A., López-Cachero, F.J., 2021. Dogs that ate plants: changes in the canine diet during the late bronze age and the first iron age in the northeast Iberian Peninsula. J. World Prehist. 34, 75–119. https://doi.org/10.1007/s10963-021-09153-9.

Alonso, N., 2000. Cultivos y producción agrícola en época ibérica. SAGVNTVM-PLAV Extra-3 25.

Amorosi, T., Buckland, P.C., Edwards, K.J., Mainland, I., McGovern, T.H., Sadler, J.P., Skidmore, P., 1998. They did not live by grass alone: the politics and palaeoecology of animal fodder in the North Atlantic region. Environ. Archaeol. 1 (1), 41–54. https://doi.org/10.1179/env.1996.1.1.41.

Andugar, L., Saña, M., 2004. La gestió ramadera durant el segon mil·lenni raco.cat/index.php/Cypsela/article/ view/175787. Cypsela 15, 209–228. https://raco.cat/index.php/Cypsela/article/view/175787.

Balasse, M., Ambrose, S.H., Smith, A.B., Price, T.D., 2002. The seasonal mobility model for prehistoric herders in the south-western Cape of South Africa assessed by isotopic analysis of sheep tooth enamel. J. Archaeol. Sci. 29 (9), 917–932. https://doi.org/10.1006/jasc.2001.0787.

Balasse, M., Tresset, A., Ambrose, S.H., 2006. Stable isotope evidence (δ13C, δ18O) for winter feeding on seaweed by Neolithic sheep of Scotland. J. Zool. 270 (1), 170–176. https://doi.org/10.1111/j.1469-7998.2006.00104.x.

Balasse, M., Tresset, A., Obein, G., Fiorillo, D., Gandois, H., 2019. Seaweed-eating sheep and the adaptation of husbandry in Neolithic Orkney: new insights from Skara Brae. Antiquity 93 (370), 919–932. https://doi.org/10.15184/aqy.2019.95.

Bender, M.M., 1971. Variations in the $^{13}C/^{12}C$ ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. Phytochemistry 10 (6), 1239–1244. https://doi.org/10.1016/S0031-9422(00)84324-1.

Blanz, M., Mainland, I., Richards, M., Balasse, M., Ascough, P., Wolfhagen, J., Taggart, M.A., Feldmann, J., 2020. Identifying seaweed consumption by sheep using isotope analysis of their bones and teeth: Modern reference δ13C and δ15N values and their archaeological implications. J. Archaeol. Sci. 118, 105140. https://doi.org/10.1016/j.jas.2020.105140.

Bogaard, A., Heaton, T.H., Poulton, P., Merbach, I., 2007. The impact of manuring on nitrogen isotope ratios in cereals: archaeological implications for reconstruction of diet and crop management practices. J. Archaeol. Sci. 34 (3), 335–343. https://doi.org/10.1016/j.jas.2006.04.009.

Bouso, M., Fernández, M.J., Gago, N., Pons, E., 2000. La producción agrícola y la transformación y conservación de cereales en Mas Castellar-Pontós. III Reunió sobre Economia en el Món Ibèric. SAGVNTVM-PLAV Extra-3.

Bouso M, Buxó R, Fernández MJ, Fuertes M, Garcia JP, Gonzalo C, López A, Pons E, Rovira N, Vargas A (2002) Reflexions finals. In: Pons E (ed) Mas Castellar de Pontós (Alt Empordà). Un complex arqueològic d'època ibèrica (Excavacions 1990-1998). Girona, Sèrie Monogràfica 21. Museu d'Arqueologia de Catalunya, pp. 587-596.

Britton, K., Müldner, G., Bell, M., 2008. Stable isotope evidence for salt-marsh grazing in the Bronze Age Severn Estuary, UK: implications for palaeodietary analysis at coastal sites. J. Archaeol. Sci. 35 (8), 2111–2118. https://doi.org/10.1016/j.jas.2008.01.012.

Brown, W.B., Christofferson, P.V., Massler, M., Weiss, M.B., 1960. Postnatal tooth development in cattle. Am. J. Vet. Res. 21 (80), 7–34.

Canal, D., 2000. Dieta vegetal y explotación agraria en el mundo ibérico a través del análisis de semillas y frutos: el Mas Castellar de Pontós. SAGVNTVM-PLAV Extra-3.

Canal D (2002) L'explotació dels recursos vegetals: les anàlisis carpològiques. In: Pons, E (ed) Mas Castellar de Pontós (Alt Empordà). Un complex arqueològic d'època ibèrica (Excavacions 1990-1998). Girona, Sèrie Monogràfica 21. Museu d'Arqueologia de Catalunya, pp. 443-476.

Casals FR (2007) Els aiguamolls. Un paisatge genuïnament empordanès. Annals de l'Institut d'Estudis Empordanesos:63-71.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363. https://doi.org/10.1007/s00442005086.

Colominas L (2008) Els animals en el conjunt de les pràctiques socials desenvolupades a l'establiment rural de Mas Castellar (Pontòs, Girona). Cypsela: revista de prehistòria i protohistòria 17:219-232.

Colominas L (2013) Arqueozoología y Romanización. Producción, distribución y consumo de animales en el noreste de la península ibérica entre los siglos V ane- V dne. British Archaeological Reports British Series 2480, Oxford: Archaeopress.

Colominas, L., 2017. Using faunal remains to evaluate social stratification in the Middle Iron Age. the fortified village of Mas Castellar de Pontós, north-east Iberian Peninsula. In: Rowley-Conwy, P., Halstead, P., Serjeantson, D. (Eds.), Economic Zooarchaeology: Studies in Hunting, Herding and Early Agriculture. Oxbow books, Oxford & Philadelphia, pp. 269–278.

Colominas L, Olesti O (2025) Producción y consumo de recursos ganaderos. In: Carreras C, Molina J, Olesti O, Revilla V (eds) *Economía de la Hispania romana. Paisajes de producción y dinámicas comerciales* (vol. 16), Universitat de Barcelona Edicions, Barcelona, pp. 291-338.

Columella LC De re rustica.

El Shaer, H.M., 2006. Halophytes as cash crops for animal feeds in arid and semi-arid regions. In: Öztürk, M., Waisel, Y., Khan, M.A., Görk, G. (Eds.), Biosaline Agriculture and Salinity Tolerance in Plants. Birkhäuser Basel, Basel, pp. 117–128. https://doi.org/10.1007/3-7643-7610-4_13.

El Shaer, M.H., Attia-Ismail, S.A., 2002. Halophytes as animal feeds: Potentiality, constraints, and prospects. In: In: Proceedings of the International Symposium on Optimum Utilization in Salt Affected Ecosystems in Arid and Semi-Arid Regions, pp. 411–418.

Ejarque, A., Julià, R., Ree, J.M., Mesquita-Joanes, F., Marco-Barba, J., Riera, S., 2016. Coastal evolution in a Mediterranean microtidal zone: Mid to Late Holocene natural dynamics and human management of the Castelló lagoon. NE Spain. Plos One 11 (5), e0155446. https://doi.org/10.1371/journal.pone.0155446.

Evans, F.D., Critchley, A.T., 2014. Seaweeds for animal production use. J. Appl. Phycol. 26 (2), 891–899. https://doi.org/10.1007/s10811-013-0162-9.

Fabre, M., Forest, V., Ranché, C., Fiorillo, D., Casabianca, F., Vigne, J.D., Balasse, M., 2023. Milk and meat exploitation, autumn lambing and use of forest resources in Neolithic Corsican sheep farming systems (fifth to third millennia cal BC). J. Archaeol. Sci. Rep. 50, 104037. https://doi.org/10.1016/j.jasrep.2023.104037.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Biol. 40 (1), 503–537. https://doi.org/10.1146/annurev. pp. 40.060189.002443.

Feranec, R.S., MacFadden, B.J., 2006. Isotopic discrimination of resource partitioning among ungulates in C3-dominated communities from the Miocene of Florida and California. Paleobiology 32 (2), 191–205. https://doi.org/10.1666/05006.1.

Friedli, H., Lötscher, H., Oeschger, H., Siegenthaler, U., Stauffer, B., 1986. Ice core record of the 13C/12C ratio of atmospheric CO2 in the past two centuries. Nature 324 (6094), 237–238.

Fuertes M, Gonzalo C, González H, López A, Pons E, Rodrigo E, Rovira N, Vargas A, Teixidor E (2002) L'establiment rural. In: Pons E (ed) Mas Castellar de Pontós (Alt Empordà). Un complex arqueològic d'època ibèrica (Excavacions 1990-1998). Girona, Sèrie Monogràfica 21. Museu d'Arqueologia de Catalunya, pp. 97-163.

Gallego, A., Rivals, F., Palet, J.M., 2017. Pastando en las marismas. Una aproximación desde la técnica del microdesgaste dentario a la alimentación del ganado ovino en el Empordà romano (noreste de la Península Ibérica). Pyrenae 48 (1), 93–113. https://doi.org/10.1344/Pyrenae2017.vol48num1.4.

Gat, J.R., 1980. The isotopes of hydrogen and oxygen in precipitation. In: Fritz, P., Fontes, J.C. (Eds.), Handbook of Environmental Isotope Geochemistry. the Terrestrial Environment 1. Elsevier, Amsterdam, pp. 21–42. https://doi.org/10.1007/1-4020-3023-1_4.

Gesti, J., 2006. El Poblament Vegetal Dels Aiguamolls De L'empordà. Arxius De La Secció De Ciències., Vol. CXXXVIII. Institut d'Estudis Catalans, Barcelona.

Gracia F (2005) El món ibèric al nord-est peninsular: panorama actual de la recerca. In: Buch J (ed). Món ibèric als Països Catalans: XIII Col·loqui Internacional d'Arqueologia de Puigcerdà. Homenatge a Josep Barberà i Farràs. Puigcerdà, 14 i 15 de novembre de 2003. Institut d'Estudis Ceretans, pp. 203-216.

Grant A (1982) The use of tooth wear as a guide to the age of domestic ungulates. In: Wilson B, Grigson C, Payne S (eds) Ageing and sexing animal bones from archaeological sites. BAR Publishing, pp 91-108.

Hasnain, M., Abideen, Z., Ali, F., Hasanuzzaman, M., El-Keblawy, A., 2023. Potential of halophytes as sustainable fodder production by using saline resources: a review of current knowledge and future directions. Plants 12 (11), 2150. https://doi.org/10.3390/plants12112150.

Hemminga, M.A., Mateo, M.A., 1996. Stable carbon isotopes in seagrasses: variability in ratios and use in ecological studies. Mar. Ecol. Prog. Ser. 140, 285–298. https://doi.org/10.3354/meps140285.

Houérou, H.L., 1994. Forage halophytes and salt-tolerant fodder crops in the Mediterranean Basin. In: Squires, V., Ayoub, A.T. (Eds.), Halophytes as a Resource for Livestock and for Rehabilitation of Degraded Lands, Vol. 32. Springer Science & Business Media, pp. 123–137. https://doi.org/10.1007/978-94-011-0818-8.

Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatite. Rev. Mineral. Geochem. 48 (1), 455–488. https://doi.org/10.2138/rmg.2002.48.12.

Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo) ecology and (paleo) climate. Proc. Natl. Acad. Sci. 107 (46), 19691–19695. https://doi.org/10.1073/pnas.1004933107.

Lavin, S., Massagué, E., Ruiz, J., Vigo, M., 1993. L'aprofitament dels recursos animals. Els humans en els àmbits ecològics del món. Mediterrànies 5, 284–327.

Lee-Thorp, J.A., Van der Merwe, N., 1987. Carbon isotope analysis of fossil bone apatite. S. Afr. J. Sci. 83 (11), 712–715.

Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochim. Cosmochim. Acta 48 (2), 385–390. https://doi.org/10.1016/0016-7037(84)90259-X.

Luz, B., Kolodny, Y., Horowiyz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochim. Cosmochim. Acta 48 (8), 1689–1693. https://doi.org/10.1016/0016-7037(84)90338-7.

Makkar, H.P., Tran, G., Heuzé, V., Giger-Reverdin, S., Lessire, M., Lebas, F., Ankers, P., 2016. Seaweeds for livestock diets: a review. Anim. Feed Sci. Technol. 212, 1–17. https://doi.org/10.1016/j.anifeedsci.2015.09.018.

Marino, B.D., McElroy, M.B., 1991. Isotopic composition of atmospheric CO2 inferred from carbon in C4 plant cellulose. Nature 349 (6305), 127–131. https://doi.org/10.1038/349127a0.

Marziale MV Epigrammaton.

Mateu, A.I., 1992. A revised list of the European C_4 plants. Photosynthetica (praha) 26 (3), 323–331.

Messana, C., 2024. Tales of sheep in the north-eastern Iberian Peninsula during the Iron Age (3rd century BC): a multi-isotope research. Universitat Rovira i Virgili, Tarragona. PhD thesis.

Messana, C., Tornero, C., Colominas, L., 2023. Choose what suits you the best: reproductive patterns and livestock management in the Iron Age Iberian Peninsula (3rd c. In: BC). Archaeological and Anthropological Sciences 15(5):56. https://doi.org/10.1007/s12520-023-01752-1.

Messana, C., Tornero, C., Colominas, L., 2025. Beyond the herd: investigating livestock feeding strategies in the Iron Age Iberian Peninsula (3rd c. BC) through a multi-isotope analysis. Archaeol. Anthropol. Sci. 17 (1), 1–31. https://doi.org/10.1007/s12520-024-02116-z.

Navarrete, V., Vaccaro, I., Escribá, P., Grau, E., García-Puchol, O., Bernabeu Aubán, J., 2025. Isotopes, herds, and landscape management practices: New insights on early farming communities in the Serpis Valley (Eastern Iberian Peninsula). PLoS One 20 (6), e0325137. https://doi.org/10.1371/journal.pone.0325137.

Pons E, Asensio D, Fuertes M, Bouso M (2010) El yacimiento del Mas Castellar de Pontós (Alt Empordà, Girona): un núcleo indígena en la órbita de la colonia focea de Emporion. In: Tréziny H (ed) Grecs et indigènes de la Catalogne à la mer Noire. Aix-en-Provence: BIAMA 3, Centre Camille Jullian, pp. 105-118. doi: 10.4000/books.pccj.350.

Pyankov, V.I., Ziegler, H., Akhani, H., Deigele, C., Luettge, U., 2010. European plants with C4 photosynthesis: geographical and taxonomic distribution and relations to climate parameters. Bot. J. Linn. Soc. 163 (3), 283–304. https://doi.org/10.1111/j.1095-8339.2010.01062.x.

Raven, J.A., Johnston, A.M., Kübler, J.E., Korb, R., McInroy, S.G., Handley, L.L., Scrimgeour, C.M., Walker, D.I., Beardall, J., Vanderklift, M., Fredriksen, S., Dunton, K.H., 2002. Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. Aust. J. Plant Physiol. 29 (3), 355–378. https://doi.org/10.1071/PP01201.

Rey-Crespo, F., López-Alonso, M., Miranda, M., 2014. The use of seaweed from the Galician coast as a mineral supplement in organic dairy cattle. Animal 8 (4), 580–586. https://doi.org/10.1017/S1751731113002474.

Ros MT, Piqué R (2002) El paisatge del Mas Castellar entre els S. VI-II a de C.: Avaluació de les dades antracològiques. In: Pons E (ed) Mas Castellar de Pontós (Alt Empordà). Un complex arqueològic d'època ibèrica (Excavacions 1990-1998). Girona, Sèrie Monogràfica 21. Museu d'Arqueologia de Catalunya, pp. 443-476.

Salazar-García, D.C., 2009. Estudio de la dieta en la población neolítica de Costamar: Resultados preliminares de análisis de isótopos estables de Carbono y Nitrógeno. In: Ruiz, J.M. (Ed.), Torre La Sal (ribera De Cabanes. Castellón), Evolución del paisaje antrópico desde la Prehistoria hasta el Medioevo. Servei d'Investigacions Arqueològiques i Prehistòriques, pp. 411–418.

Salazar García, D.C., 2011. Aproximación a la dieta de la población calcolítica de La Vital a través del análisis de isótopos estables del carbono y del nitrógeno sobre restos óseos. In: Pérez Jordà, G., Bernabeu Aubán, J., Carrión Marco, Y., García Puchol, O., Molina Balaguer, L., Gómez Puche, M. (Eds.), La Vital (gandia. Valencia), Vida y muerte en la desembocadura del Serpis durante el III y el I milenio aC. Museu de Prehistòria de València, pp. 139–143 http://hdl.handle.net/10550/42608.

Sanmartí, J., 2014. L'Estat del coneixement sobre la cultura ibèrica a Catalunya. Butlletí De La Societat Catalana D'estudis Històrics 25, 227–260. https://doi.org/10.2436/20.1001.01.131.

Sanmartí J (2021) Breu història de la investigación. In: Museu d'Arqueologia de Catalunya (ed) L'enigma iber: arqueologia d'una civilització. Departament de Cultura. Generalitat de Catalunya, pp. 23-30.Strabo GIC Geographica.

Stringi, L., Giambalvo, D., Amato, G., Di Miceli, G., 2009. Productivity of an Atriplex halimus shrubbery and effects of grazing on lambs. Ital. J. Anim. Sci. 8 (sup2), 549–551. https://doi.org/10.4081/ijas.2009.s2.549.

Tieszen LL, Boutton TW (1989) Stable carbon isotopes in terrestrial ecosystem research In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological research. New York, NY: Springer New York, pp. 167-195. DOI: 10.1007/978-1-4612-3498-2_11.

Tieszen, L.L., 1991. Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. J. Archaeol. Sci. 18 (3), 227–248. https://doi.org/10.1016/0305-4403(91)90063-U.

Tornero, C., Bălăşescu, A., Ughetto-Monfrin, J., Voinea, V., Balasse, M., 2013. Seasonality and season of birth in early Eneolithic sheep from Cheia (Romania): methodological advances and implications for animal economy. J. Archaeol. Sci. 40 (11), 4039–4055. https://doi.org/10.1016/j.jas.2013.05.013.

Von Bertalanffy, L., 1968. General system theory. N. Y. 41973 (1968), 40.

Walker, D.J., Lutts, S., Sánchez-García, M., Correal, E., 2014. Atriplex halimus L.: its biology and uses. J. Arid Environ. 100, 111–121. https://doi.org/10.1016/j.jaridenv.2013.09.004.

Walsh, K., Knockaert, J., Dulias, K., Giguet-Covex, C., Unsain, D., Burri, S., Magniez, P., Pike, A., Orton, D., Mocci, F., 2023. Bioarchaeological approaches to understanding the long-term development of mountain societies. Archaeol. Anthropol. Sci. 15 (12), 199. https://doi.org/10.1007/s12520-023-01889-z.