

This is a repository copy of Early Dalmatian farmers specialized in sheep husbandry.

White Rose Research Online URL for this paper: https://eprints.whiterose.ac.uk/id/eprint/202566/

Version: Published Version

Article:

Sierra, A., Balasse, M., Radović, S. et al. (3 more authors) (2023) Early Dalmatian farmers specialized in sheep husbandry. Scientific reports. 10355. ISSN: 2045-2322

https://doi.org/10.1038/s41598-023-37516-z

Reuse

This article is distributed under the terms of the Creative Commons Attribution (CC BY) licence. This licence allows you to distribute, remix, tweak, and build upon the work, even commercially, as long as you credit the authors for the original work. More information and the full terms of the licence here: https://creativecommons.org/licenses/

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



scientific reports



OPEN

Early Dalmatian farmers specialized in sheep husbandry

A. Sierra^{1,2\infty}, M. Balasse¹, S. Radović³, D. Orton⁴, D. Fiorillo¹ & S. Presslee^{4,5}

The spread of farming in the central and western Mediterranean took place rapidly, linked to the Impressa Ware. The Impressa Ware originated somewhere in the southern Adriatic and spread westwards across the Mediterranean. These early farmers had an economy based on cereal agriculture and caprine husbandry, but there is still little information on how this agropastoral system functioned. This study aims to unravel the farming practices of the early Dalmatian farmers linked to the Impressa culture by using an integrated analysis, combining archaeozoology, palaeoproteomics and stable isotopes, applied to the faunal assemblages of Tinj-Podlivade and Crno Vrilo. The results show: (1) the composition of the flocks was overwhelmingly sheep; (2) sheep exploitation at both sites was similar, focusing on milk and meat; (3) sheep reproduction was concentrated at the beginning of winter, with no reproduction in autumn as in later sites in the western Mediterranean. We conclude that a common animal economy existed at both sites, which could be related to the mobility practiced by these early farming societies throughout the Mediterranean.

The spread of the Neolithic in Europe has given rise to very different agropastoral systems throughout time and space in response to environmental and sociocultural factors. The primary spread of these practices across Europe involved two main routes: one around the central and western Mediterranean coast, linked to Impressa pottery, and another through the Danube basin into central Europe, linked to Starčevo–Körös–Criş (SKC) and eventually Linearbandkeramik (LBK) pottery¹. The major differences between these two primary routes have been highlighted².³ but variability within each of those has not been fully explored. This necessitates, beyond the constitution of the herds, describing carefully how these animals were managed, including the orientation of production as revealed by mortality profiles and the seasonal rhythms of these pastoral systems.

The Adriatic is a key area for the neolithization of the central and western Mediterranean. The 'maritime' stream, linked to the so-called Impressa Ware, first became clearly distinct in this area. This style originated in the southern Adriatic somewhere between Tavoliere and Dalmatia⁴ and its dissemination was fast, with contemporary dates from the beginning of the 6th millennium cal BC on both coasts^{5,6}. Different dynamics have been observed for the eastern Adriatic, depending on the previous presence of hunter-gatherers⁷. While in the north (Istria) and south (southern Dalmatia) the occupation of caves previously occupied by hunter-gatherers has been detected, in central Dalmatia the presence of abundant open-air settlements has been documented. Despite this, most of the neolithisation models put forward^{5,7,8} agree that the colonizing groups played an important role in establishing the Neolithic way of life.

The Impressa Ware cultural complex is characterized by a mixed economy based on cereal agriculture⁹ and livestock farming dominated by caprines and with little importance of hunting^{2,3,10-13}. Within the caprine category, most archaeozoological work has emphasised a predominance of sheep over goats in Impressa herds^{14,15}. However, because these two species have different adaptations and potential, it is necessary to define more precisely the ratio of sheep to goats in these herds. New methods, such as improved osteological criteria^{16,17} and palaeoproteomic analyses¹⁸⁻²⁰, provide the opportunity to define with greater certainty the extent to which sheep predominate. The application of Zooarchaeology by Mass Spectrometry (ZooMS) allows sheep and goat to be differentiated due to a difference in peptide markers between the two species¹⁹. In addition, a better knowledge of the composition of the herds also allows a better characterisation of how the animals were reared. One of the important aspects is demographic management, including reproductive management, which is entirely related to the production strategy and the seasonal management of production. The application of stable isotope analysis to investigate sheep birthing season is a way to approach the rhythms of these systems. Although autumn lambing

¹AASPE «Archéozoologie, Archéobotanique: Sociétés, Pratiques, Environnements» CNRS, MNHN, 75005 Paris, France. ²Departament de Prehistoria, Facultat de Lletres, Universitat Autonoma de Barcelona, Bellaterra, Barcelona, Spain. ³Croatian Academy of Sciences and Arts, Institute for Quaternary Palaeontology and Geology, Ante Kovačića 5, 10000 Zagreb, Croatia. ⁴BioArCh, Department of Archaeology, Environment Building, University of York, Heslington, York YO10 5NG, UK. ⁵Department of Chemistry, University of York, Heslington, York YO10 5NG, UK. ⁶Demail: asierrasainzaja@gmail.com

has been demonstrated in the northwestern Mediterranean at sites post-dating the Impressa^{21–23} (Cardial complex), in stark contrast to spring lambing elsewhere in Europe²⁴, this key parameter had not yet been explored in the Impressa.

Materials

Sites. The eastern Adriatic coast is a region bounded to the west and south by the Adriatic Sea, and to the north and east by the Dinaric Alps which separate it from the rest of the Balkan Peninsula It is a karst landscape dominated by mountains rising steeply from the coast. In the middle is the Ravni Kotari region, which consists of an alternating series of valleys and low ridges, where farmers have settled since the early Neolithic²⁵. In this area are the Tinj-Podlivade and Crno Vrilo sites, among the most important open-air sites in the Adriatic, with the presence of Early Neolithic occupations, and whose faunal collections are among the most abundant and best-preserved (Fig. 1).

Tinj-Podlivade is located in a secondary basin between the Vrana depression to the southwest and mountain range to the northeast, at an altitude of 50 m above sea level. The excavation was carried out by a British-Yugoslav team in 1984^{26} . The site occupied an area of 2.8 ha. Two sectors (A and B) were excavated and a stratigraphic sequence of 0.75 m in thickness was documented, with built structures and four pits. Three conventional radiocarbon dates have dated the occupation of this site to the beginning of the 6th millennium BC (5815-5185 cal BC), but with a high standard deviation 18 . The present study has re-dated the sheep T Ovis 44 which confirms the antiquity of the site (ICA-14C-6145: 6900+/-60 BP; 5908-5666 calBC at 95.4% probability). The major component of the ceramic assemblages is pottery with impressed decoration. Agriculture is also well documented from the cultivation of three different species of cereals 27 (barley, emmer and einkorn). In addition, a significant number of weed seeds were documented. The 15,365 recovered faunal remains stand out as undoubtedly one of the most quantitatively important in this geographical area for this chronology. Of these Schwartz dientified a total of 3212 remains. The assemblage is mainly composed of caprine remains (91.4%), with the sheep/goat ratio not being given. Among the other domestic species recovered, remains of cattle, pigs and dogs are also recorded, but in small numbers. Hunting of wild resources is a minor component (included birds and molluscs). These data have led to propose that the economic model of the site was a lowland mixed farming economy 26 .

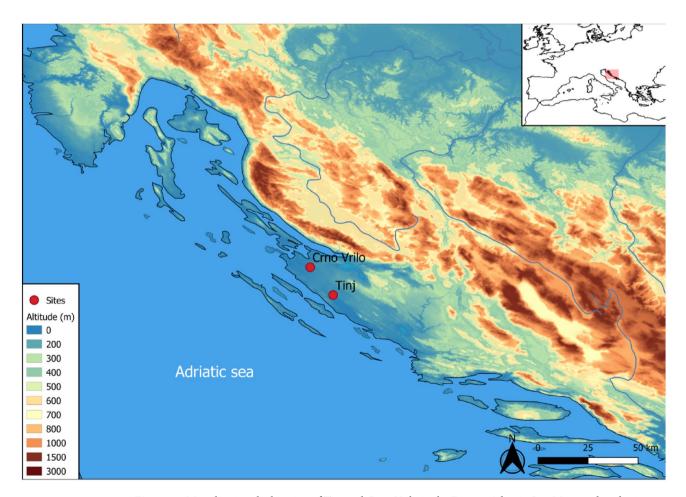


Figure 1. Map showing the location of Tinj and Crno Vrilo in the Eastern Adriatic Sea. Map produced using QGis 3.10.4

Crno Vrilo is located on the right side of the Miljašić Jaruga River, about 12 km from the modern town of Zadar. It was excavated between 2001 and 2005 by members of the University of Zadar²⁵. The Neolithic settlement was located 63 m above sea level and covered an area of 6750-7500 m², of which 550 m² were excavated. The cultural layer starts at the surface and has an average thickness of about 0.6 m, overlying the bedrock. The deposits were divided into several excavated layers, but it is regarded as a single-layered site with only a single cultural phase²⁵. Excavation has documented constructional remains of dwellings (hearths, ovens, stone walls and posts). Available dating also places it in the Early Neolithic period, with dates around the first half of the 6th millennium BC25. The material culture is very rich, with abundant remains of pottery with impressed decoration, flint and bone tools. Archaeobotanical data show a predominance of cereals, followed by leguminous plants (Fabaceae). Emmer and einkorn wheat (Triticum dicoccon and Triticum monococcum) and barley (Hordeum vulgare) are documented²⁹. From an archaeozoological point of view, the site is very rich, dominated by mammals (NISP = 3564) and molluscs (n = 4217). Among the marine fauna, molluscs stand out, with a wide variety of species such as the mussel (Mytilus galloprovincialis) and the oyster (Oestra edulis)³⁰. Among the macromammals, the largest component is also sheep and goat (95.94%)³¹, with the presence of cows, pigs and wild mammals being very low. The abundance and variety of bird species is also noteworthy. In short, Crno Vrilo would have a mixed farming economy in which the surrounding alluvial areas would be exploited ²⁵.

Samples. *Mortality profiles and ZooMS analysis.* For the elaboration of the Tinj and Crno Vrilo mortality profiles, the mandibles and the loose lower dental remains were used. In the case of Tinj, all the dental remains were analysed. For Crno Vrilo, only the material from Trench A was analysed due to the large size of the total faunal assemblage. All caprine teeth and mandibles from this trench have been studied in detail by one of the authors (S.R.) during his PhD thesis³¹. For the purpose of this study, we have rechecked all original identifications in terms of taxa and age assessment. Only some minor inaccuracies were noted and corrected.

The dental remains of caprines were analysed trying to separate sheep and goats morphologically whenever possible ^{16,17,32–35}. Among a total of 428 mandibles and dental remains, 193 were selected for ZooMS analysis, including 122 from Crno Vrilo and 71 from Tinj. Of these, 164 correspond to all remains certainly belonging to distinct individuals and morphologically identified as sheep, goat or caprine. A further 29 loose teeth were also selected to corroborate that there was no different representation between these elements.

Stable oxygen isotope analysis. A total of 23 lower third molars were selected for isotope analysis, out of the remains attributed to sheep according to the morphological criteria mentioned above, and confirmed as *Ovis aries* by ZooMS analysis. Sixteen samples are from Crno Vrilo and 7 are from Tinj. Most of them were slaughtered between 24 and 72 months (Table 1).

ID	Species ZooMS	Tooth	Side	Age class (*) (*according to Payne 1973)	Estimated age (*) (*according to Payne 1973)	¹⁴ C date
T63 Ovis	Ovis aries	M_3	R	Е	2-3 y	
T9 Ovis	Ovis aries	M_3	R	Е	2-3 y	
T76 Ovis	Ovis aries	M_3	L	G	4-6 y	
T8 Ovis	Ovis aries	M_3	L	G	4-6 y	
T48 Ovis	Ovis aries	M_3	L	G	4-6 y	
T47 Ovis	Ovis aries	M_3	L	G	4-6 y	
T44 Ovis	Ovis aries	M_3	R	G	4-6 y	5908-5666 calBC
CV32 Ovis	Ovis aries	M_3	L	D	12-24 m	
CV136 Ovis	Ovis aries	M_3	L	Е	2-3 y	
CV129 Ovis	Ovis aries	M_3	L	Е	4-6 y	
CV125 Ovis	Ovis aries	M_3	L	F	3-4 y	
CV137 Ovis	Ovis aries	M_3	L	F	3-4 y	
CV113 Ovis	Ovis aries	M_3	L	F	3-4 y	
CV149 Ovis	Ovis aries	M_3	L	F	3-4 y	
CV69 Ovis	Ovis aries	M_3	L	G	4-6 y	
CV52 Ovis	Ovis aries	M_3	L	G	4-6 y	
CV72 Ovis	Ovis aries	M_3	L	G	4-6 y	
CV122 Ovis	Ovis aries	M_3	L	G	4-6 y	
CV97 Ovis	Ovis aries	M_3	L	G	4-6 y	
CV41 Ovis	Ovis aries	M_3	L	G	4-6 y	
CV112 Ovis	Ovis aries	M_3	L	G	4-6 y	
CV43 Ovis	Ovis aries	M_3	L	G	4-6 y	
CV42 Ovis	Ovis aries	M_3	L	G	4-6 y	

Table 1. Samples selected for isotopes analysis.

Results

ZooMS results. All dental remains were analysed using morphological criteria prior to applying the ZooMS methodology, trying to separate sheep and goats $^{16,17,32-35}$. A total of 428 mandible and teeth (including 281 from Crno Vrilo and 147 from Tinj) were analysed (Fig. 2). From osteological criteria, a majority of these remains were attributed to sheep (79% at Crno Vrilo and 60% at Tinj) and a minority to goats (13% at Crno Vrilo and 20% at Tinj). However, a significant percentage of remains could not be classified (8% at Crno Vrilo and 20% at Tinj). This was because they were loose teeth on which the reliability of the identification criteria is lower 16 , especially the fourth deciduous premolar (dP_4).

Among the 193 samples analysed with ZooMS, 187 were positive and could be separated into sheep and goats. Only 6 were negative due to poor preservation. Out of 187 positive samples (132 being previously identified as sheep, 31 as goats and 24 were unidentified), 186 were identified as sheep and only one—from Tinj—as a goat.

If we compare the results of the morphological identification with those of ZooMS, we can see that although the archaeozoological methods allow us to identify the predominance of sheep, goats tend to be over-represented. In addition, the limitations of the methods (fragmentation, loose teeth, teeth with poorly discriminating criteria, etc.) leave a percentage of individuals unclassified that ZooMS allows us to identify.

No differences were observed between loose teeth and mandibles in those teeth that were misidentified (Table 2). In terms of individual teeth, the P4 generated problems in identifying sheep and goats, with 47.1% of the remains being misidentified. The dP_4 also generated identification problems, 37.7% of the remains could not be identified, most of them loose. As for molars, only 21.4% have been misidentified.

Mortality profiles. Since 99% of the remains analysed with ZooMS belong to sheep, it has been assumed that most of the teeth belong to sheep and the mortality profile has been performed using all the teeth (Fig. 3). The mortality profile of Tinj is characterised by the presence of juveniles and young adults, between 6 and 24 months (age classes C to D). On the other hand, there is also the presence of adult classes, between 24 months and 6 years (age classes EF to G). Finally, the low presence of the youngest classes, which correspond to animals

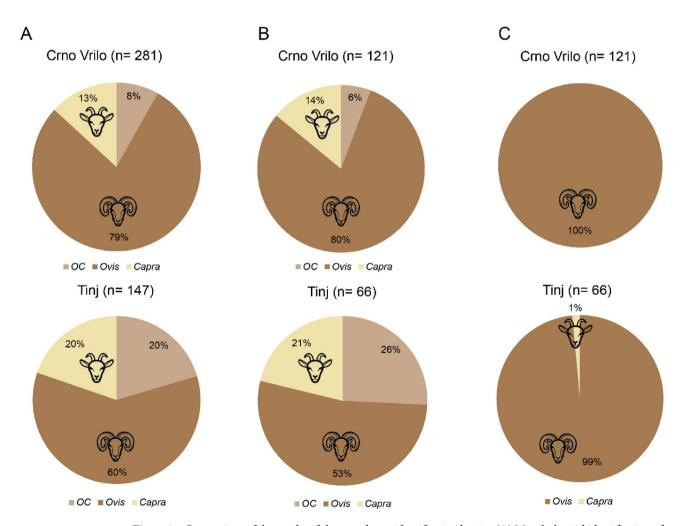


Figure 2. Comparison of the results of sheep and goat identification by site. **(A)** Morphological identification of all analysed remains. **(B)** morphological identification of the remains analysed by ZooMS. **(C)** identification by ZooMS.

	Loose	Mandible	dP ₄	P ₄	M ₁₋₃
Ovis	67	65	38	18	103
Capra	13	18	0	16	24
Ovis/Capra	19	5	23	0	4
%misidentified	32.3%	25.3%	37.7%	47.1%	21.4%

Table 2. Morphological identification by type of remains of samples identified as *Ovis* by ZooMS. Left: comparison of mandibles and loose teeth. Right: comparison by teeth (count has been made for each tooth of the jaw, so their sum is greater than the total number).

aged between 0 and 6 months, is noteworthy. The absence of these animals may be due to problems of preservation of these remains as they are younger or because the animals could birth in another area.

The caprine mortality profile of Crno Vrilo is very similar to that of Tinj. Dead animals between 6 and 12 months are very abundant. Other very frequent age classes are D, between 12 and 24 months, and EF, between 24 months and 4 years. Finally, like Tinj, there is a noteworthy absence of the younger classes, due to possible reasons mentioned above. In any case, the presence among the bones of some perinatal animals confirms their presence at the site³¹.

Stable isotope analysis. Oxygen isotope ratios. The results from the measurements of stable oxygen isotope ratios are shown in Table 3 and Fig. 4. Overall, the δ^{18} O values vary between – 5.4 and 3.1‰. The midrange δ^{18} O value (max+min/2) varies between – 3.6 and 0.3‰, and the amplitude of intra-tooth variation is between 3.4 and 5.7‰. The intra-tooth δ^{18} O sequences measured in the M3 vary according to a sinusoidal pattern, which probably reflects the seasonal cycle, with the lowest values in the cold season (winter) and the highest in the warm season (summer).

Modelling of the $\delta 18O$ sequences. Results from the modelling of the $\delta 18O$ sequences and the normalized location in tooth crown of the $\delta 18O$ sequence optimum (x_0/X) are shown in Fig. 5. T8 Ovis, T48 Ovis, T47 Ovis, CV32 Ovis and CV149 Ovis could not be modelled because their sequences were truncated. At Tinj, x_0/X ratios for 4 sheep vary between 0.08 and 0.25, defining a breeding period of 0.17 year (around 2 months). At Crno Vrilo, the length of the breeding period, estimated from the analysis of 14 sheep, is 0.5 years (around 6 months), with x_0/X ratios varying between 0.98 (or - 0.02) and 0.48. However, at this site, most individuals (n = 10) have x_0/X ratios between 0.98 and 0.15, defining a main breeding period of 0.17 years (2 months).

Discussion

Sheep specialization. The application of paleoproteomic identification (ZooMS) to separate sheep and goats—the first such application for the Adriatic region—has shown that practically all the specimens analysed are *Ovis aries*. This indicates that the early Dalmatian herds were composed almost entirely of sheep, implying a strong specialization in sheep husbandry among the early Adriatic farming communities. If this is the case in Dalmatia at such an early date and close to the beginning of the Impressa current, one wonders to what extent this could be the norm during the Neolithic in other nearby regions. Moreover, taking into account the results of this work showing the over-representation of goats and the loss of information due to the lack of classification of some individuals, one might also wonder whether the sheep/goat ratios for the period are at all reliable. The results have shown that teeth such as dP_4 and P_4 generate problems in separating sheep and goats. These problems have already been pointed out by previous studies, especially for dP_4^{16} . Therefore, these problems should be taken into account when separating sheep and goats, in order to avoid introducing a bias in the interpretation of flock composition in the past.

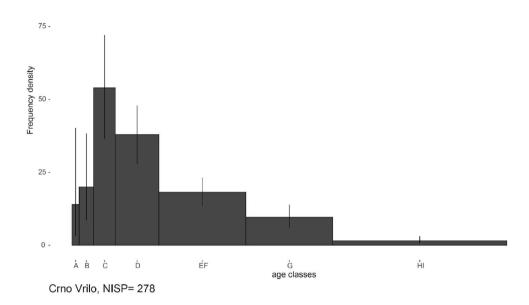
Specialization in particular livestock has both economic and social implications. Halstead³⁸ has proposed that livestock farming focused on a single species reduces the security of the herd and the variety of available products. In addition, specialization would be linked to large-scale herding³⁸ and even altitudinal mobility for the Mediterranean³⁹. But, why would the first farmers have such heavily sheep-based husbandry?

One of the first reasons we could propose is ecological. The Mediterranean environment has particular characteristics, with mild rainy winters and hot and dry summers⁴⁰. This could have made difficult the adaptation of some domestic species with higher resource requirements for their survival, such as cattle. However, some of the recent meta-analyses conducted on the Balkan and Mediterranean region have shown that variation in animal management could not be explained by adaptation to the environment alone³, and environment cannot explain the preference for sheep over goats.

Another explanation for this specialization, related to the previous one, could be economic. The sheep could have been a very important animal economically for the first farmers. This species provides a multitude of products with higher nutritional values than goats^{41–43}. This would lead to a preference in the first herds over the latter species.

In addition, sheep-centered animal husbandry may have social implications. Animal resources can become vehicles of enduring social relations⁴⁴, and may have a social value that goes beyond the economic one^{45,46}. This social value of sheep may have been present in Adriatic farming societies, explaining the specialisation in this species. This special value is difficult to unravel with current data, but the appearance in the subsequent Danilo





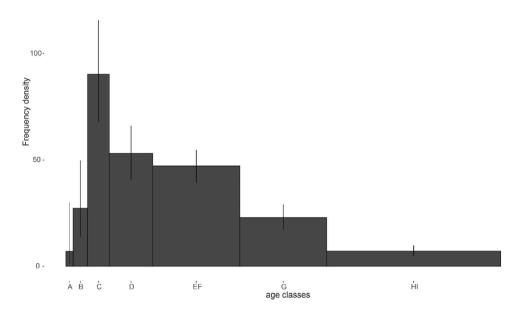


Figure 3. Mortality profiles in Tinj and Crno Vrilo, based on NISP, with 95% credible intervals of the frequency density (see 30). Age classes: A (0–2 months), B (2–6 months), C (6–12 months), D (12–24 months), EF (24–48 months), G (48–72 months) and HI (>72 months).

period of objects such as rhytons (zoomorphic-shaped vessels documented from the Middle Neolithic onwards) may be indicators of the importance of sheep beyond the economic role⁴⁷.

Finally, specialisation could be explained by the way the farming economy spread in the northern Mediterranean. Specialization in sheep has been observed also in sites related to Impressa pottery in Italy and southern France^{14,48}, so it seems to be linked with the early Neolithic communities of the central and western Mediterranean. Current archaeological data show a rapid diffusion of farming communities related to the Impressa complex⁴⁵. This rapid diffusion must have taken place by sea^{46,49} using boats of different types. This navigation

		$d^{18}O_{\mathrm{VPDB}}$				
	n	Max	Min	Mid-range	Amplitude	
T Ovis 76	20	- 0.52	- 4.7	- 2.60	4.17	
T Ovis 8	13	- 0.41	- 2.78	- 1.59	2.37	
T Ovis 48	15	- 1.60	- 3.93	- 2.77	2.33	
T Ovis 47	17	0.54	- 2.55	- 1.01	3.09	
T Ovis 44	15	- 0.57	- 4.17	- 2.37	3.60	
T Ovis 63	19	0.68	- 3.92	- 1.62	4.60	
T Ovis 9	18	0.18	- 4.36	- 2.09	4.54	
CV Ovis 69	17	0.86	- 4.65	- 1.90	5.52	
CV Ovis 52	18	- 1.58	- 4.87	- 3.22	3.29	
CV Ovis 136	21	0.11	- 5.35	- 2.62	5.46	
CV Ovis 72	17	- 0.08	- 3.19	- 1.63	3.11	
CV Ovis 125	19	0.25	- 5.12	- 2.44	5.37	
CV Ovis 32	16	- 1.92	- 4.43	- 3.17	2.51	
CV Ovis 122	20	- 0.78	- 4.97	- 2.88	4.20	
CV Ovis 137	19	0.04	- 4.05	- 2.00	4.09	
CV Ovis 113	17	3.11	- 3.70	- 0.30	6.81	
CV Ovis 97	18	0.16	- 3.66	- 1.75	3.82	
CV Ovis 41	17	- 0.35	- 4.66	- 2.51	4.31	
CV Ovis 129	18	0.72	- 3.90	- 1.59	4.62	
CV Ovis 112	16	- 0.34	- 4.41	- 2.38	4.07	
CV Ovis 43	16	1.10	- 4.17	- 1.54	5.27	
CV Ovis 42	17	- 0.31	- 3.81	- 2.06	3.50	
CV Ovis 149	19	- 0.03	- 2.86	- 1.45	2.83	
Min		- 1.92	- 5.35	- 3.64	3.43	
Max		3.11	- 2.55	0.28	5.66	

Table 3. Results from stable oxygen (δ 18O) analysis of enamel bioapatite. Specimen, tooth, maximum (max) and minimum value (min), mid-range and amplitude of intra-tooth variation (A).

would be supported for the Adriatic case by the occupation of the Adriatic islands⁵⁰ and by the presence of artifacts made with flint from Gargano, southern Italy^{51,52}. Navigation has also been previously documented for the settlement of Cyprus⁵³ and the island of Crete⁵⁴. Therefore, sheep specialization may have had to do with an anticipatory mobility strategy⁵⁵ in which human communities carried out a strategy adapted to navigation^{10,56,57}. Both sheep and goats could be the perfect animal to transport in a first colonization because of their light weight, reproductive capacity and the variety of products they can bring to these communities, but, in addition, the docility of sheep could have played a role in their favour. Thus, building on the argument of Zilhao⁴⁹ for caprines in general, the first farmers could have focused on one species with many advantages for both travel and settlement to increase the chances of successful travel.

Any of these proposals could be plausible with the present data, and several or all of them could have occurred together. In this respect, the continuity of specialization in caprines (possibly sheep) in Dalmatia beyond the early Neolithic is striking^{2,3}. The initial specialization could be explained by the Neolithic diffusion, as observed in Greece in previous centuries, where livestock farming was very much centred on caprine animals (especially sheep), but cattle and, above all, pigs were more important in quantitative terms than in Dalmatia⁵⁸. This importance would acquire social and/or ideological aspects in later periods, as demonstrated by the widespread diffusion of zoomorphic (*rhyton*) vessels from the Middle Neolithic onwards⁴⁷.

Sheep products. The combination of ZooMS and mortality profiles has allowed us to obtain reliable mortality profiles for sheep. The mortality profiles of Tinj and Crno Vrilo show the predominant culling of young animals, between 6 and 24 months of age, but also the maintenance of quite a few animals beyond 24 and even 48 months. These data allow us to propose a mixed exploitation of sheep, with slaughtering aimed at both milk and meat production. On the one hand, the slaughter of animals in age classes C (6–12 m) and D (12–24 m) corresponds to the exploitation of meat before it reaches its optimal meat weight. In fact, the abundant presence of animals slaughtered before the first year of life would show an interest in the exploitation of tender meat. On the other hand, keeping animals beyond 24 months of age would correspond to the exploitation of milk and meat, since animals would be slaughtered when their productivity declines^{59–62}. Payne's⁶³ model for milk proposes the culling of newborn animals to avoid competition for milk between the offspring and the human group. However, these are theoretical models that would correspond to optimization for a single objective, and farmers oriented towards mixed meat and milk production tend to postpone slaughtering to exploit meat⁶⁴. This would be the case in Tinj and Crno Vrilo, where milk would be exploited and, in addition, lambs would be kept after weaning for meat production. Dairy production has been previously proposed in the Adriatic from osteo-

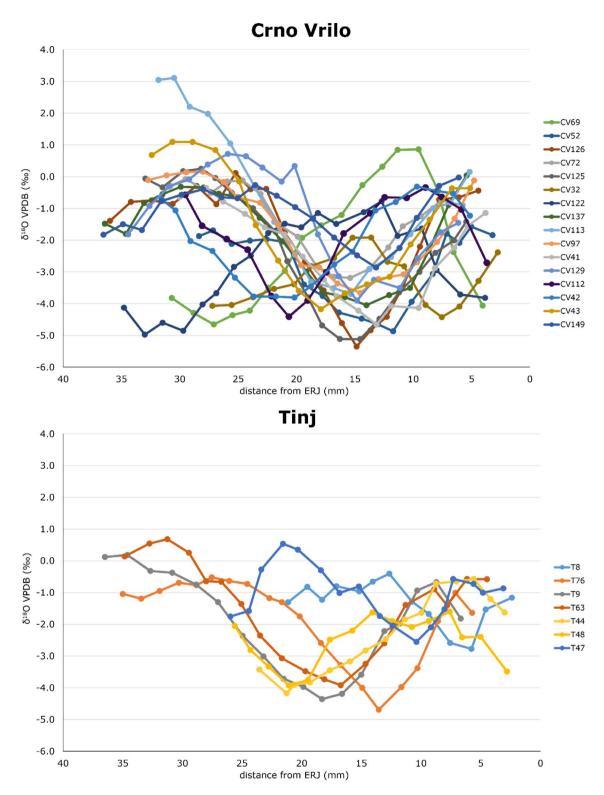


Figure 4. Results from the sequential stable oxygen isotope analysis in third molar (M3) enamel bioapatite. Each sample is located in the tooth crown relative to its distance from the enamel-root junction (ERJ).

logical analyses ^{10,31,56,57} and was confirmed by ceramic residue analyses both in the area⁶⁵ and throughout the Mediterranean ^{10,66}. Another aspect that is noteworthy is the abundant presence of animals slaughtered beyond 48 months at the Crno Vrilo site. This fact can have several explanations, the first of them would be related to the aforementioned exploitation of milk. In addition, animals can be kept alive longer to benefit from their manure production, as has been demonstrated for the Neolithic in other areas of the Mediterranean⁶⁷. Finally, another explanation could be the search for herd security, minimizing herd fluctuations ^{41,42}.

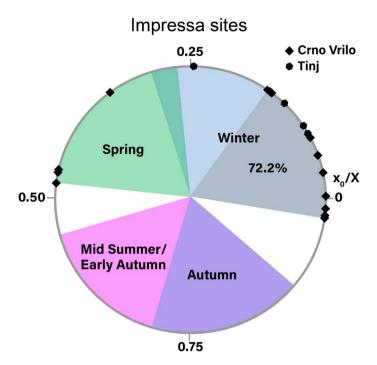


Figure 5. Distribution of sheep births at Tinj and Crno Vrilo, as reflected by the position of the maximum δ^{18} O value in tooth crown (×0) normalized to the period of the cycle (X). The birth season is compared with modern reference sheep (Carmejane CAR³⁶; Rousay ROU²⁴, Le Merle and La Fage³⁷). Blue, green, purple and pink color areas represent ×0/X ratios obtained from modern specimens.

In summary, the mortality profiles of Tinj and Crno Vrilo are very similar to each other. Considering that the differences are very slight, a similar exploitation strategy can be assumed for both sites. This strategy seems to be related to the conformation of the herds. Within this unity, the strategy could have multiple explanations such as those mentioned above (economic, social or cultural).

Sheep reproduction. A main lambing period in early winter is different from what has been documented up to now in Neolithic Europe: in temperate Europe the dominant pattern is late winter/spring births^{24,37}. Early winter births are documented in the Early and Middle Neolithic in the northwestern Mediterranean^{21,22,68,69} but in association with autumn lambing. Autumn lambing in the northwestern Mediterranean is explained by a capacity of Mediterranean breed for out-of-season breeding (an extended fertility period or less intense sexual rest)^{70,71} and manipulation by the herders who separate females and males and reintroduce males only in the spring to obtain autumn births.

Early winter as the main lambing period at Crno Vrilo and Tinj could be due to an extended period of fertility in these ewes (starting earlier compared to sheep at higher latitude in Europe) and no manipulation by the herders to delay breeding to the spring. An early mating (end of summer instead of autumn) could lead to early winter lambing. Winter births are common among current Mediterranean sheep husbandry systems and especially among Dalmatian autochthonous breeds^{72–74}. The concentration of births in early winter could mean a rather good fertility rate (most females become pregnant at the beginning of the breeding period) while the (rather isolated) spring births could also be the sign of females failing in their pregnancy (losing their foetus for example) and getting fertilized again before the end of the fertility period.

The short lambing period is also a common livestock strategy among different pastoral groups, as mentioned by Tornero et al. 75 for Southwest Asia, Bernus 76 for the Sahel or as collected by sources for Mesopotamia at the end of the 3rd millennium BC 77 .

In summary, the data present in this study show that early winter lambing is favoured in Dalmatia, while autumn lambing is not documented until the introduction of sheep in the western Mediterranean. This could mean that there was already a capacity for a prolonged period of fertility in the ewes, but without manipulation by the herders. However, this would be advantageous for the herders. On the one hand, winter lambing may be partly related to the availability of pasture. The Mediterranean climate is characterized by dry summers and mild, wet winters. Thus, from autumn onwards, when rainfall increases⁴⁰, pasture availability is higher in winter than in summer^{78–80}. In addition, winter births favor milk production compared to spring births. It has been shown that climate can have adverse effects on milk production and milk quality^{81,82}. The high temperatures of the Mediterranean climate negatively affect milk production, so the breeding season would be a fundamental aspect. This is the case for the autochthonous breeds of the study area, whose productivity increases in ewes lambing between autumn and winter⁸³. The birth of most of the lambs in a short period of time would make it possible to organize the work within the annual cycle. The lambing period involves a lot of work for the herders, since they have to guarantee the survival of the lambs⁸⁴. Moreover, this possible livestock calendar could be well

articulated with the agricultural calendar, taking into account that the main crops of both sites are cereals^{27,29} that would be grown in winter and harvested in spring⁸⁵. Finally, the anticipated mobility strategy proposed above would also be favoured by the birth of lambs in a short period of time. If the strategy of human groups is to plan mobility between areas, the concentration of births in a short space of time and in a period of difficult maritime mobility can be fundamental.

Conclusion

The integrated archaeozoological, palaeoproteomic and isotopic results have allowed us to elucidate the practices of the first farmers in Dalmatia, linked to the Impressa Ware. The archaeozoological data indicated that livestock farming in the area was centred on caprine herds. This work, applying the ZooMS method for the first time in the region, has made it possible to reconstruct demographically the composition of these herds, showing that they were overwhelmingly composed of sheep, with very few goats present. Mortality profiles have shown a very similar exploitation of sheep for Tinj and Crno Vrilo, with meat and milk being the main products exploited. Finally, the data on sheep reproduction show that most of the births of sheep in both sites were concentrated at the beginning of winter, which contrasts with the data from the western Mediterranean for the Early Neolithic 21,22,68,69

The integration of the results shows how in these two sites the early Dalmatian farmers, linked to the Impressa Ware, had a common animal economy. First of all, the conformation of the livestock herds at the two analysed sites was similar, with sheep as the main animal. Moreover, the sheep herds were exploited in a similar way, with a common breeding management. This common animal economy in both sites seems to indicate a cultural unity beyond the Impressa pottery. Early Dalmatian farmers had an economy based on the exploitation of sheep for products such as milk and meat with an early winter birth period which would have favoured production and would have been ideal for organising all the tasks of the annual cycle. Moreover, this common strategy could be related to the mobility practised by these early farming societies of the Impressa Ware throughout the Mediterranean. In any case, it will be important for future work to examine other sites around the Adriatic with the same methods, to assess whether our results are specific to these two Dalmatian sites or represent a consistent pattern of early Neolithic animal management across the wider region.

Methods

Mortality profiles. The estimation of the age at death was based on the study of dental remains, mainly from the analysis of tooth eruption and wear patterns. Data on tooth eruption and wear were recorded following Payne 63,86 , also using his age classes. In addition, these data were supplemented with metric data from the method of Helmer 87 based on the decrease of the crown height (H/DT) with age.

Mortality profiles were then constructed following the method of Gerbault et al.⁸⁸ which uses the Dirichlet distribution to construct histograms with Bayesian credible intervals that allow us to increase our ability to differentiate between age class representations within an archaeological assemblage. The 'rdirichlet' function of the R package LaplacesDemon (v. 4.1.3) was used for this purpose.

ZooMS. ZooMS analysis was carried out on 193 mandibular and dental remains. Samples of between 10 and 30 mg were taken and demineralised by adding 250 μl of 0.6 M hydrochloric acid to the bone and left at 4 °C for approximately 2 days until the bone became flexible. To remove any possible contaminants, the remaining bone was rinsed once with 250 μl of 0.1 M sodium hydroxide and three times with 50 mM ammonium bicarbonate (NH4HCO3) buffer pH 8.0 (Ambic). The bone was then gelatinised in a heating block at 65 °C in 100 μl of Ambic for 1 h. A 50 μl aliquot of the supernatant was transferred to a new tube, to which 1 μl of 0.5 μg μl⁻¹ trypsin was added, and the solution was left for 18 h in a 37 °C heating block. After stopping trypsin digestion by adding 1 μL of 5% trifluoroacetic acid (TFA), the peptides were extracted and purified using 100 μL of Pierce C18 ZipTips with washing (0.1% TFA and UHQ water) and conditioning (0.1% TFA in 50:50 acetonitrile and UHQ water) solutions. 1 μL of the sample was spotted in triplicate on a MALDI 384 plate with 1 μL of α-cyano-4-hydroxycinnamic acid matrix solution and air dried. MALDI analysis was carried out using a Bruker Ultraflex III MALDI-TOF mass spectrometer at the University of York. Replicates were averaged using the open-source software mMass (www.mmass.org; 81) and compared to a database of known m/z markers $^{18-20}$.

Oxygen isotopes. For the study of reproduction, stable oxygen isotope analysis (δ^{18} O) was performed on tooth enamel bioapatite. Following the procedure described in Balasse et al.⁸⁹, sequential sampling was performed on the buccal side of the molar, in the middle lobe of M3. The enamel surface was cleaned by abrasion using a tungsten drill. Enamel was sampled sequentially perpendicularly to the tooth growth axis from the apex to the enamel-root junction using a diamond drill bit. Samples were spaced at 1–1.5 mm intervals. A low magnification lens (\times 3) was used throughout the sampling process. The samples were located in the tooth crown using their distance from the enamel-root junction. The samples were then pre-treated for 4 h in 0.1 M acetic acid [CH3COOH] (0.1 ml of solution/0.1 mg of sample). The weight loss caused by this pretreatment was 29.5 \pm 6%.

The pre-treated enamel powders were analysed on a Kiel IV device connected to a DeltaVAdvantage IRMS. The accuracy and precision of the measurements were verified using an internal laboratory calcium carbonate standard (Marbre LM standardised according to the international standard NBS 19). The results are expressed in V-PDB. The analytical precision, estimated from four to eight Marbre LM analyses, was on average 0.03% for δ^{18} O values and 0.02% for δ^{13} C values. Over the period of analysis of the enamel samples, the analysis of 102 Marbre LM gave an average δ^{18} O value of $-2.03\pm0.1\%$ (expected value = -1.83%).

The δ^{18} O sequences were modelled using an equation derived from a cosine function described in Balasse et al. ⁹⁰ using four parameters: the position of the maximum value of δ^{18} O (×0); the cycle period (X; distance

over which an annual cycle was recorded); the signal amplitude (A) and the mean (M). The cycle period (X) was used to normalise \times 0 to remove inter-individual variability in tooth size⁸³. The ratio \times 0/X varies with season of birth. Season of birth is estimated by comparison with reference \times 0/X ratios obtained in modern sheep^{24,37}. All results are shown using a circular representation to reflect the cyclical nature of seasonality²⁴.

Data availability

All data generated or analyzed during this study are included in this published article [and its supplementary information files].

Received: 19 February 2023; Accepted: 22 June 2023

Published online: 26 June 2023

References

- 1. Bocquet-Appel, J. P., Naji, S., Vander Linden, M. & Kozlowski, J. K. Detection of diffusion and contact zones of early farming in Europe from the space-time distribution of 14C dates. *J. Archaeol. Sci.* 36, 807–820 (2009).
- 2. Orton, D., Gaastra, J. & Vander Linden, M. Between the Danube and the deep blue sea: Zooarchaeological meta-analysis reveals variability in the spread and development of neolithic farming across the western Balkans. *Open Quat* 2, 1–26 (2016).
- Gaastra, J. S. & Vander Linden, M. Farming data: Testing climatic and palaeoenvironmental effect on Neolithic Adriatic stockbreeding and hunting through zooarchaeological meta-analysis. Holocene 28, 1181–1196 (2018).
- 4. Forenbaher, S. & Miracle, P. T. Transition to farming in the Adriatic: A view from the eastern shore. In *The Neolithic Transition in the Mediterranean* (eds Guilaine, J. et al.) 233–241 (Editions Errance, 2014).
- 5. Forenbaher, S., Kaiser, T. & Miracle, P. T. Dating the East Adriatic Neolithic. Eur J Archaeol 16, 589–609 (2013).
- 6. Binder, D. et al. Modelling the earliest north-western dispersal of Mediterranean Impressed Wares: New dates and Bayesian chronological model. *Documenta Praehistorica* 44, 54–77 (2017).
- 7. Forenbaher, S. & Miracle, P. T. The spread of farming in the Eastern Adriatic. Documenta Praehistorica 33, 89-100 (2006).
- 8. Bass, B. The maritime expansion of Early Neolithic agro-pastoralism in the eastern Adriatic Sea. *tti della Società per la Preistoria e Protostoria della Regione Friuli-Venezia Giulia XIV* **2003**, 45–60 (2004).
- Gaastra, J. S., de Vareilles, A. & Vander Linden, M. Bones and seeds: An integrated approach to understanding the spread of farming across the Western Balkans. Environ. Archaeol. 27, 44–60 (2022).
- Debono Spiteri, C. et al. Regional asynchronicity in dairy production and processing in early farming communities of the northern Mediterranean. Proc. Natl. Acad. Sci. USA 113, 13594–13599 (2016).
- 11. McClure, S. B. & Podrug, E. Villages, landscapes, and early farming in northern Dalmatia. in Fresh Fields and Pastures New: Papers Presented in Honor of Andrew MT Moore 117–144 (Sidestone, 2016).
- 12. Moore, A. The spread of farming to the Adriatic: New insights from Dalmatia. Euras. Prehist. 11, 155-164 (2015).
- 13. Moore, A. Early Farming in Dalmatia: Pokrovnik and Danilo Bitinj: Two Neolithic Villages in South-East Europe (Archaeopress, 2019).
- 14. Tresset, A. & Vigne, J. Substitution of species, techniques and symbols at the Mesolithic-Neolithic transition in Western Europe. *Proc. Br. Acad.* **144**, 189–210 (2007).
- 15. McClure, S. B. *et al.* The Zooarchaeology of Neolithic farmers: Herding and hunting on the Dalmatian coast of Croatia. *Quatern. Int.* **634**, 27–37 (2022).
- 16. Zeder, M. A. & Pilaar, S. E. Assessing the reliability of criteria used to identify mandibles and mandibular teeth in sheep, Ovis, and goats, Capra. J. Archaeol. Sci. 37, 225–242 (2010).
- 17. Gillis, R., Chaix, L. & Vigne, J. D. An assessment of morphological criteria for discriminating sheep and goat mandibles on a large prehistoric archaeological assemblage (Kerma, Sudan). *J. Archaeol. Sci.* 38, 2324–2339 (2011).
- 18. Buckley, M., Collins, M., Thomas-Oaies, J. & Wilson, J. C. Species identification by analysis of bone collagen using matrix-assisted laser desorption/ionisation time-of-flight mass spectrometry. *Rapid Commun. Mass Spectrom.* 23, 3843–3854 (2009).
- 19. Buckley, M. et al. Distinguishing between archaeological sheep and goat bones using a single collagen peptide. J. Archaeol. Sci. 37, 13–20 (2010).
- 20. Buckley, M. & Collins, M. J. Collagen survival and its use for species identification in Holocene-lower Pleistocene bone fragments from British archaeological and paleontological sites. *Antiqua* 1, e1 (2011).
- 21. Tornero, C. *et al.* Early evidence of sheep lambing de-seasoning in the Western Mediterranean in the sixth millennium BCE. *Sci. Rep.* **10**, 12798 (2020).
- 22. Tejedor-Rodríguez, C. et al. Investigating Neolithic caprine husbandry in the Central Pyrenees: Insights from a multi-proxy study at Els Trocs cave (Bisaurri, Spain). PLoS ONE 16, e0244139 (2021).
- 23. Sierra, A. et al. Sheep husbandry in the early Neolithic of the Pyrenees: New data on feeding and reproduction in the cave of Chaves. *J. Archaeol. Sci. Rep.* 37, 102935 (2021).
- 24. Balasse, M. et al. Neolithic sheep birth distribution: Results from Nova Nadezhda (sixth millennium BC, Bulgaria) and a reassessment of European data with a new modern reference set including upper and lower molars. J. Archaeol. Sci. 118, 105139 (2020).
- 25. Marijanović, B. Crno Vrilo 1. (Sveučilište u Zadru, Odjel za Arheologiju, 2009).
- 26. Chapman, J., Shiel, R. & Batović, Š. *The changing face of Dalmatia* (Leicester University Press, 1996).
- 27. Huntley, J. The plant remains. In The Changing Face of Dalmatia (eds Chapman, J. et al.) 187–189 (Leicester University Press, 1996).
- Schwartz, C. The faunal remains. In The Changing Face of Dalmatia (eds Chapman, J. et al.) 186–187 (Leicester University Press, Berlin, 1996).
- 29. Šoštarić, R. Karbonizirani ostaci žitarica–tragovi poljodjelstva. In *Crno vrilo*, 2 (ed. Marijanović, B.) 49–52 (Sveušilište u Zadru, 2009).
- 30. Vujčić-Karlo, S. Nalazi mekušaca (Mollusca). In Crno Vrilo 2 (ed. Marijanović, B.) 77–87 (Sveušilište u Zadru, 2009).
- 31. Radovic, S. Ekonomija prvih stočara na istočnom Jadranu: značenje lova i stočarstva u prehrani neolitičkih ljudi. (University of Zagreb, 2011).
- 32. Balasse, M. & Ambrose, S. H. Distinguishing sheep and goats using dental morphology and stable carbon isotopes in C4 grassland environments. *J. Archaeol. Sci.* 32, 691–702 (2005).
- 33. Halstead, P., Collins, P. & Isaakidou, V. Sorting the sheep from the goats: Morphological distinctions between the mandibles and mandibular teeth of adult Ovis and Capra. *J. Archaeol. Sci.* 29, 545–553 (2002).
- 34. Helmer, D. Discrimination des genres Ovis et Capra à l'aide des prémolaires inférieures 3 et 4 et interprétation des âges d'abattage: l'exemple de Dikili Tash (Grèce). Anthropozoologica 31, 29–38 (2000).
- 35. Payne, S. Morphological distinctions between the mandibular teeth of young sheep, Ovis, and goats, Capra. J. Archaeol. Sci. 12, 139–147 (1985).
- 36. Blaise, E. & Balasse, M. Seasonality and season of birth of modern and late Neolithic sheep from south-eastern France using tooth enamel δ18O analysis. *J. Archaeol. Sci.* **38**, 3085–3093 (2011).

- 37. Balasse, M., Chemineau, P., Parisot, S., Fiorillo, D. & Keller, M. Experimental data from lacaune and merino sheep provide new methodological and theoretical grounds to investigate autumn lambing in past husbandries. *J. Archaeol. Method Theory* https://doi.org/10.1007/s10816-022-09600-7 (2023).
- 38. Halstead, P. Pastoralism or household herding? Problems of scale and specialization in early Greek animal husbandry. World Archaeol. 28, 20–42 (1996).
- 39. Halstead, P. Traditional and ancient rural economy in Mediterranean Europe: plus ça change?. J. Hell Stud. 107, 77-87 (1987).
- 40. Combourieu-Nebout, N. et al. Holocene vegetation and climate changes in the central Mediterranean inferred from a high-resolution marine pollen record (Adriatic Sea). Clim. Past 9, 2023–2042 (2013).
- 41. Redding, R. W. Decision Making in Subsistence Herding of Sheep and Goats in the Middle East (University of Michigan, 1981).
- 42. Redding, R. Theoretical determinants of a herder's decisions: Modeling variation in the sheep/goat ratio. in *Animals and Archaeology 3*, Early Herders and their Flocks (eds. Clutton-Brock, J. & Grigson, C.) 223–242 (British Archaeological Reports 202, 1984).
- 43. Jandal, J. M. Comparative aspects of goat and sheep milk. Small Rumin. Res. 22, 177-185 (1996).
- 44. Ingold, T. Hunters, Pastoralists and Ranchers: Reindeer Economies and Their Transformations (Cambridge University Press, 1980).
- 45. Manen, C. et al. The Neolithic transition in the Western Mediterranean: A complex and non-linear diffusion process—The radiocarbon record revisited. *Radiocarbon* 61, 531–571 (2019).
- Rowley-Conwy, P. Westward Ho!: The spread of agriculture from central Europe to the Atlantic. Curr. Anthropol. 52, 5431–5451 (2011).
- Mlekuž, D. 'Sheep are your mother': Rhyta and the interspecies politics in the Neolithic of the eastern Adriatic. Documenta Praehistorica 34, 267–280 (2007).
- 48. Rowley-Conwy, P., Gourichon, L., Helmer, D. & Vigne, J.-D. Early domestic animals in Italy, Istria, the Tyrrhenian Islands and Southern France. In *The Origins and Spread of Domestic Animals in Southwest Asia and Europe* (eds Colledge, S. et al.) 161–194 (Left Coast Press, 2013).
- Zilhão, J. Early prehistoric navigation in the Western Mediterranean: Implications for the Neolithic transition in Iberia and the Maghreb. in Proceedings of the Wenner Gren Foundation Workshop on Island Archaeology and the Origins of Seafaring in the Eastern Mediterranean, Eurasian Prehistory, Vol 11, (eds. Ammerman, A. & Davis, T.) 185–200 (Jagiellonia University, 2014).
- 50. Forenbaher, S. The earliest islanders of the eastern Adriatic. Coll. Antropol. 23, 521-530 (1999).
- 51. Forenbaher, S. Trans-Adriatic contacts and the transition to farming. Euras. Prehist. 15, 25-46 (2019).
- 52. Kačar, S. The Neolithisation of the Adriatic: Contrasting regional patterns and interactions along and across the shores. *Open Archaeol.* 7, 798–814 (2021).
- Vigne, J.-D. & Cucchi, T. Premières navigations au Proche-Orient: les informations indirectes de Chypre. Paléorient 31, 186–194 (2005).
- 54. Broodbank, C. & Strasser, T. F. Migrant farmers and the Neolithic colonization of Crete. Antiquity 65, 233-245 (1991).
- 55. Kent, S. The relationship between mobility strategies and site structure. *The interpretation of archaeological spatial patterning* 33–59 (1991). https://doi.org/10.1007/978-1-4899-2602-9_3.
- 56. Miracle, P. & Pugsley, L. Vertebrate Faunal Remains from Pupićina Cave. in *Prehistoric Herders of Northern Istria: the Archaeology of Pupićina Cave* (eds. Miracle, P. & Forenbaher, S.) vol. 1 259–399 (Arheološki muzej Istre, 2006).
- Legge, A. & Moore, A. Clutching at straws: The early neolithic of croatia and the dispersal of agriculture. in *The Dynamics of Neolithisation in Europe: Studies in Honour of Andrew Sherrat* (eds. Hadjikoumis, A., Robinson, E. & Viner, S.) 176–195 (Oxbow Books, 2011).
- 58. Halstead, P. & Isaakidou, V. Early stock-keeping in Greece. in *The origins and spread of domestic animals in Southwest Asia and Europe* (eds. Colledge, S., Conolly, J., Dobney, K., Manning, K. & Shennan, S.) 129–144 (Left Coast Press, 2013).
- 59. Helmer, D. & Vigne, J.-D. La gestion des cheptels de caprinés au Néolithique dans le midi de la France. in Approches Fonctionnelles en Préhistoire, Actes du XXVe Congrès Préhistorique de France Nanterre 24–26 novembre 2000 (2004).
- Vigne, J.-D. & Helmer, D. Was milk a "secondary product" in the Old World Neolithisation process? Its role in the domestication of cattle, sheep and goats. Anthropozoologica 42, 9–40 (2007).
- 61. Helmer, D., Gourichon, L. & Vila, E. The development of the exploitation of products from Capra and Ovis (meat, milk and fleece) from the PPNB to the Early Bronze in the northern Near East (8700. *Anthropozoologica* 42, 41–69 (2007).
- 62. Blaise, É. Référentiel actuel de brebis «Préalpes du Sud» (Digne, Alpes-de-Haute-Provence, France): pratiques d'élevage et âges dentaires. *Anthropozoologica* 41, 191–214 (2006).
- 63. Payne, S. Kill-off patterns in sheep and goats: The Mandibles from Asvan Kale. Anatol. Stud. 23, 281-303 (1973).
- Halstead, P. Mortality models and milking: Problems of uniformitarianism, optimality and equifinality reconsidered. Anthropozoologica 27, 3–20 (1998).
- 65. McClure, S. B. *et al.* Fatty acid specific δ13C values reveal earliest Mediterranean cheese production 7,200 years ago. *PLoS ONE* 13, e0202807 (2018).
- 66. Evershed, R. P. et al. Dairying, diseases and the evolution of lactase persistence in Europe. Nature 608, 336–345 (2022).
- 67. Vaiglova, P. et al. An integrated stable isotope study of plants and animals from Kouphovouno, southern Greece: A new look at Neolithic farming. J. Archaeol. Sci. 42, 201–215 (2014).
- 68. Martín, P., Tornero, C., García, D. C. S. & Vergès, J. M. Early sheep herd management in the inland of the Iberian Peninsula: Results of the incremental isotopic analyses of dental remains from El Mirador cave (Sierra de Atapuerca, Spain). *Archaeol. Anthropol. Sci.* 13, 1–18 (2021).
- 69. Fabre, M. et al. Nouvel éclairage sur les systèmes d'élevage ovins du Chasséen: Reproduction, alimentation et productions animales à Auriac, Carcassonne (Aude, France). In Biodiversités, environnements et sociétés depuis la préhistoire: nouveaux marqueurs et approches intégrées (eds Nicoud, E. et al.) 101–112 (Éditions APDCA, 2021).
- 70. Forcada, F., Abecia, J. A. & Sierra, I. Seasonal changes in oestrus activity and ovulation rate in Rasa Aragonesa ewes maintained at two different body condition levels. *Small Rumin. Res.* 8, 313–324 (1992).
- 71. Gómez-Brunet, A., Santiago-Moreno, J., Toledano-Diaz, A. & López-Sebastián, A. Reproductive seasonality and its control in Spanish sheep and goats. *Trop. Subtrop. Agroecosyst.* **15**, S47–S70 (2012).
- 72. Špehar, M., Mulc, D., Barać, Z., Mioć, B. & Kasap, A. Estimation of genetic parameters for dairy traits in Pag sheep with single and multi-trait test-day models. *Small Rumin. Res.* **183**, 106029 (2020).
- 73. Kasap, A. et al. The impact of age at first lambing on milk yield and lactation length in a population of Istrian sheep under semi-intensive management. Animals 11, 1604 (2021).
- 74. Vince, S. et al. Determination of physiological particularities of the sexual cycle and breeding season of Pramenka breed. Veterinarska Stanica 48, 13–24 (2017).
- 75. Tornero, C., Balasse, M., Molist, M. & Saña, M. Seasonal reproductive patterns of early domestic sheep at Tell Halula (PPNB, Middle Euphrates Valley): Evidence from sequential oxygen isotope analyses of tooth enamel. J. Archaeol. Sci. Rep. 6, 810–818 (2016).
- 76. Bernus, E. Seasonality, climatic fluctuations, and food supplies (Sahelian nomadic pastoral societies). In *Coping with Uncertainty in Food Supply* (eds de Garine, I. & Harrison, G.) 318–336 (Clarendon Press, 1987).
- 77. Widell, M. Destined for slaughter: Identifying seasonal breeding patterns in sheep and goats in early Babylonia. *J. Near East. Stud.* **79**, 209–223. https://doi.org/10.1086/710168 (2020).
- 78. Martin, G. B. et al. Non-photoperiodic inputs into seasonal breeding in male ruminants. In *Perspectives in Comparative Endocrinology* (eds Davey, K. et al.) 574–585 (National Research Council of Canada, 1994).

- 79. Todaro, M. et al. Aseasonal sheep and goat milk production in the Mediterranean area: Physiological and technical insights. Small Rumin. Res. 126, 59–66 (2015).
- 80. Serrano, J., Shahidian, S. & da Silva, J. M. Monitoring seasonal pasture quality degradation in the Mediterranean Montado ecosystem: Proximal versus remote sensing. *Water (Basel)* 10, 1422 (2018).
- 81. Abecia, J. A. et al. The effects of weather on milk production in dairy sheep vary by month of lambing and lactation phase. J. Anim. Behav. Biometeorol. 5, 56–63 (2017).
- 82. Gonzalez-Ronquillo, M., Abecia, J. A., Gómez, R. & Palacios, C. Effects of weather and other factors on milk production in the Churra dairy sheep breed. *J. Anim. Behav. Biometeorol.* **9**, 2125 (2021).
- 83. Kastelic, M., Špehar, M. & Barać, Z. Productivity of milk and milk composition of Istrian sheep in Croatia and Slovenia. Slov. Vet. Res. 50, 149–156 (2013).
- 84. Represa, D. Pastores de las Peñas de Cervera. Rev Folk 211, 3-25 (1998).
- 85. Fuks, D., Lister, D. L., Distelfeld, A. & Marom, N. A time to sow, a time to reap: Modifications to biological and economic rhythms in Southwest Asian plant and animal domestication. *Agronomy* 12, 1368 (2022).
- 86. Payne, S. Reference codes for wear states in the mandibular cheek teeth of sheep and goats. J. Archaeol. Sci. 14, 609-614 (1987).
- 87. Helmer, D. Biometria i arqueozoologia a partir d'alguns exemples del Proxim Orient. Cota zero: revista d'arqueologia i ciència 11, 51–60 (1995).
- 88. Gerbault, P. et al. Statistically robust representation and comparison of mortality profiles in archaeozoology. J. Archaeol. Sci. 71, 24–32 (2016).
- 89. Balasse, M. Reconstructing dietary and environmental history from enamel isotopic analysis: Time resolution of intra-tooth sequential sampling. *Int. J. Osteoarchaeol.* 12, 155–165 (2002).
- 90. Balasse, M., Obein, G., Ughetto-Monfrin, J. & Mainland, I. Investigating seasonality and season of birth in past herds: A reference set of sheep enamel stable oxygen isotope ratios. *Archaeometry* 54, 349–368 (2012).

Acknowledgements

This work has been carried out under the funding of the project *Impressa sheep: husbandry practices of the first farming societies in the Eastern Adriatic* by the Fyssen Foundation. In addition, we would like to thank Natalija Čondić (Archaeological Museum of Zadar) and Dario Vujević (University of Zadar) for their support in Croatia. We would also like to thank Maria Saña (Autonomous University of Barcelona), Alfonso Abecia (University of Zaragoza) and Stašo Forenbaher (Institute for Anthropological Research, Zagreb, retired) for interesting discussions on different parts of the paper. Finally, we would like to thank Krista McGrath for the loan of the ICTA-UAB laboratories and for the laboratory support provided. Stable isotope analyses were performed at the SSMIM (MNHN, Paris).

Author contributions

We confirm that all authors have approved the final version of the manuscript and have made substantial contributions. A.S. and S.R. designed and carried out the archaeozoological analyses. A.S. and M.B. designed the isotopic analysis. D.F. provided technical support for isotope analysis. A.S. and D.O. designed the palaeoproteomical analysis. SP provided technical support for palaeoproteomical analysis. A.S., M.B., S.R. and D.O. performed the data analysis. All authors interpreted the data. All authors wrote and provided comments on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-023-37516-z.

Correspondence and requests for materials should be addressed to A.S.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit https://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2023