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Experimental Data from Lacaune and Merino Sheep Provide New Methodological and Theoretical Grounds to Investigate Autumn Lambing in Past Husbandries

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Abstract

In temperate Europe, sheep predominantly mate in autumn and lamb in the spring. In contrast, present-day Mediterranean husbandries practice autumn lambing, with benefits in terms of natural resource use and seasonal availability of animal products. Autumnal lambing is enabled by the conjunction of a capability of some Mediterranean breeds for "out-of-season" breeding, intentional scheduling by the herder, and autumnal rains providing forage resources for lactation. Autumn and winter sheep births have been demonstrated at Neolithic sites in the western Mediterranean. More works are needed to define the conditions leading to their emergence. This line of research uses oxygen isotope analysis in sheep teeth and involves modern references to define birth season. The existing references were biased in favor of winter and spring births. In this study, we enlarge them with 30 additional teeth from Lacaune and Merino sheep, including mainly summer and autumn births. Experiments were also conducted on Lacaune ewes, to address theoretical grounds on the implementation of autumn births: it implies to preserve females from conceptions by separating the sexes in autumn and re-introducing the rams among females in the spring. This second step also produces a "male effect." We show that in the Lacaune breed, the proportion of spontaneously cyclic ewes in the spring is low in the absence of males and remains minor when the ewes are left in permanent contact with rams. On the other hand, we were able to implement a highly efficient male effect using non-sexually stimulated males, demonstrating that this practice could have been implemented by Neolithic herders.

Keywords Sheep · Out-of-season breeding · Male effect · Stable oxygen isotopes · Lacaune · Merino

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Introduction

Domestication was a major transformation in relationships between humans and animals and also marked the beginning of a whole field of zootechnical knowledge. In particular, domestication induced changes in animal and plant biological rhythms, especially in their reproductive cycle (Zeder, 2015). The early history of these evolutionary processes is receiving growing attention from archaeology, as new methodological tools are providing direct evidence for these changes since prehistoric times, and new questions emerge about the environmental and anthropic forces driving them (Balasse & Tresset, 2007; Jones et al., 2008; Balasse et al., 2017; Liu et al., 2017; Tornero et al., 2020). Sheep (*Ovis aries* L.) is of particular interest in this matter. Sheep lineages initially domesticated in Southeast Anatolia around 8500 BCE were introduced to Europe through Greece and the Balkans in the early 7th millennium BCE (Peters et al., 2005; Zeder, 2008). From there, they spread both along the northern coastline of the Mediterranean and the Danubian corridor and adjacent rivers to the inland Europe (Tresset & Vigne, 2011). Along this dispersal across wide longitudinal and latitudinal gradients, sheep were adapted to a diversity of climates and landscapes bearing different constraints on their reproductive cycle in terms of photoperiod and seasonal availability of forages. Under temperate climate, modern sheep have a seasonal breeding activity (Hafez, 1952), based on an endogenous circannual rhythm mainly driven by the photoperiodic cycle via melatonin secretion (Karsch et al., 1984; Malpaux et al., 1997; Thiéry et al., 2002). This seasonal reproductive activity imposes strong constraints on the socioeconomic livestock systems of farming societies, structuring the agropastoral calendar and determining the availability of animal products during the year (Rendu, 2003; Chemineau et al., 2008). Seasonal fertility was inherited from the wild ancestor, the oriental mouflon. Present-day mouflon in the Near East (Talibov et al., 2009) as well as the European mouflon (a feral domestic sheep) found in Corsica (Pfeffer, 1967), Cyprus (Hadjisterkotis & Bider, 1993), and Sardinia (Ciuti et al., 2009) lamb over a short period in the spring. Few data are available for the birthing pattern in early Holocene mouflon as well as in early domestic sheep in southwest Asia. A short lambing period was shown for mouflon during the Late Glacial in Armenia (Tornero et al., 2016a). Pre-Pottery Neolithic sheep at Tell Halula in the Middle Euphrates Valley also show a restricted period of birth (Tornero et al., 2016b).

Today in temperate Europe, sheep predominantly mate in autumn to give birth in the spring (Hafez, 1952). In contrast, in present-day sheep husbandry systems in the Mediterranean area, lambing can also be scheduled in autumn, bringing benefits in terms of natural resource use and seasonal availability of milk and lambs (Todaro et al., 2015). While occurring only exceptionally in their wild counterparts as well as in sheep husbandries implemented further North, regular autumnal lambing in the Mediterranean area is enabled by the conjunction of three factors: (i) a physiological capability of some Mediterranean breeds for an "out-of-season" breeding, enabling spring mating and autumn lambing; this capacity has a genetic support, as demonstrated by differences between breeds and intra-breed heritability (Hanocq et al., 1999; Avdi et al., 2002); (ii) intentional scheduling by the herder, by separating females and males and reuniting them in the spring (Avdi & Chemineau 1998); this management involving a good understanding of sheep reproductive physiology; (iii) abundant forage resources to support autumn lactation: in present-day Mediterranean climate, autumnal rains create favorable conditions in this regard.

All three conditions may have early met in Neolithic times. Studies involving stable isotope analysis in archaeological sheep teeth highlight variations in the timing of sheep breeding through time (6th–3rd mil. BCE) and space along the Neolithic dispersal routes: spring lambing was demonstrated at middle-latitude sites in Europe (42°–46° N) while a later onset of the breeding season at higher-latitudes sites (59° N) is explained by different photoperiodic conditions (Balasse et al., 2017, 2020). In sharp contrast to this pattern, predominant autumn and winter sheep births are attested at early and middle Neolithic sites in southern France and the Iberian Peninsula (Tornero et al., 2020; Fabre et al., 2021; Sierra et al., 2021). Autumn births were also reported at Bronze and Iron Age sites in Central Asia (Kazakhstan; Ventresca Miller et al., 2020; Hermes et al., 2022) and at Late Bronze Age sites in the South Caucasus (Chazin, 2021), although current datasets indicate low occurrence. In our opinion, this low occurrence does not reflect the herders' strategy towards autumnal lambing. Interestingly, sites in Thrace and the Lower Danube from the earliest Neolithic cultures in Europe show a spring lambing pattern (Balasse et al., 2020) despite their location at comparable latitudes to those in the Northwestern Mediterranean showing autumn lambing. This suggests that additionally to photoperiod, other factors have been determinant, including climate, farmers' technicity, and socio-economic systems. Current sheep husbandries across the northern Mediterranean basin show great variety in their forms and goals. Autumnal lambing is not an exclusive practice, depending on multiple factors including the orientation of production, forage resources, and seasonal mobility (Brooke & Ryder, 1979). Autumnal lambing systems are therefore a demonstrative example of close interconnections between biology, environment, and technical systems. More extensive systematic research is needed to define more precisely the conditions that led to their emergence in the Mediterranean area. The production of additional zooarchaeological datasets must also be accompanied by a strengthening of the methodological and theoretical grounds supporting this research.

On a methodological level first, sheep birth seasonality is investigated through the reconstruction of the seasonal cycle record in tooth, from sequential analysis of enamel stable oxygen isotope ratios ($\delta^{18}O$). As the teeth growth timing is fixed within species, the season of birth determines the sequence of the seasonal cycle recorded in a given tooth. Interindividual variability in this record reflects births seasonality (Bryant et al., 1996a, b; Balasse et al., 2003). Depending on the best represented tooth in the assemblage, the analysis is conducted on the second (M2) or the third molar (M3). The season of birth is determined through comparison with reference data obtained from modern sheep whose season of birth is known (Balasse et al., 2012). Currently used modern reference sets are globally biased towards late winter and spring births—the currently dominant lambing season in temperate Europe (Blaise & Balasse, 2011; Balasse et al., 2012; Tornero et al., 2016a, b;

Balasse et al., 2020). As a result, from isotope analyses performed in third molars, autumn lambing can only be identified as births occurring in the opposite season to spring (Hadjikoumis et al., 2018; Fabre et al., 2021). These modern reference sets must also be enlarged in number and include a higher diversity of birth seasons and sheep breeds, to challenge the time resolution of the approach and comparability between breeds. The need to expand reference sets is particularly true for the third molar, on which they are currently very scarce (Balasse et al., 2020). Although a less regular ontogenic scheduling has been observed for the M3 compared to the M2 (Zazzo et al., 2010), focusing on the M3 is also legitimate because of the need to secure tooth identification in assemblages mostly composed of isolated teeth, where second and first molars may be mixed up. Furthermore, depending on demographic management linked to the orientation of production, younger age classes may be poorly represented, and in that case, the crowns of the second molars will be heavily worn, and the study will be conducted preferentially on the third molars.

On a theoretical level then, present-day European sheep breeds are short-day breeders: the fertility period starts in autumn and lambing occurs predominantly in late winter/spring after a 5-month gestation. Predominant autumn births within a flock can only be achieved by the voluntary manipulation of reproduction by the farmer in two successive steps. The first one is to preserve females from conceptions by separating the sexes in autumn in order to have them ready to be pregnant the next spring. Then, the second step is to re-introduce the rams among females in the spring to hope to have a maximum number of out-of-season pregnancies. The success of this second step is dependent on the ability of the breed for out-of-season mating and the intensity of sexual activity of males which produce a "male effect" by reactivating ovulations and heats in the females in sexual rest under a precise time course (Girard, 1983, Delgadillo et al., 2002; Véliz et al., 2002; Chasles et al., 2016). The question remains as to the extent to which prehistoric breeders could have used these two steps of separation of sexes in autumn followed by a male effect to produce autumn lambing.

Both these methodological and theoretical points were addressed in this study. Third molars were collected from Lacaune and Merino d'Arles sheep in order to extend the oxygen isotope reference data used to determine birth season. Experiments were conducted on Lacaune ewes to quantify the relative proportion of females spontaneously ovulating in the spring, with or without the presence of males, and the effectiveness of a male effect in terms of ovulation using non-sexually stimulated males. Indeed, sexual stimulation currently involves hormonal (melatonin) or light treatments, which were only developed within the last decades and were therefore not within the reach of the Neolithic herders.

Material and Methods

Stable Isotope Reference Set for Birth Season

The currently used modern reference sets (Table 1) are composed of sheep teeth from diverse locations including Rousay in Orkney islands (Balasse et al., 2012),

Table 1 Stable isotope reference sets for sheep birth season. References: 1, Balasse et al. (2012); 2, Blaise & Balasse (2011); 3, Tornero et al. (2013); 4, Tornero et al., (2016a, b); 5, Balasse et al. (2020); 6, Balasse et al. (2005)

Name	Sheep breed	Tooth	Birth months	Reference
Rousay (ROU)	Shetland cross	Lower M2 (N=10)	Apr/May	1
Carmejane (CAR)	Préalpes du Sud	Lower M2 (N=5)	Jan, Feb, Sept	2 and 3
Selgua (XT)	Xisqueta	Lower M2 (N=2)	October	4
Kemenez (KMZ)	Ouessant × Lande de Bretagne	Lower M2 (N=4)	Jan–March	5
Kemenez (KMZ)	Ouessant × Lande de Bretagne	Lower M3 (N=16)	Jan–Mar, May/Jun, Oct	5
Kemenez (KMZ)	Ouessant × Lande de Bretagne	Upper M3 (N=8)	Jan–March, Oct	5
North-Ronaldsay (NR)	North-Ronaldsay	Lower M3 (N=4)	April/May	6
Le Merle (MRL)	Merino d'Arles	Lower M3 (N=9)	Feb/Mar/Apr, Sept/Oct	This study
La Fage (MUT)	Lacaune	Lower M3 (N=17)	Jan, Jul, Aug, Oct, Dec	This study

Carmejane in southern France (Blaise & Balasse, 2011; Tornero et al., 2013), Selgua in north-eastern Spain (Tornero et al., 2016a, b), and Kemenez in French Brittany (Balasse et al., 2020). They include sheep from different breeds (Shetland cross, Ouessant × Lande de Bretagne, Préalpes du Sud, Xisqueta) born in late winter and spring for the majority, or in early autumn for very few of them. The bias towards late winter/spring births is particularly true for the third molar (M3) with only one representative of an autumn birth in the Kemenez reference set (Balasse et al., 2020). In this study, we extend these modern references with sheep of the Lacaune and Merino d'Arles breeds, born in various seasons, with an emphasis on autumn births (September to December). The study material includes the molars from 21 sheep from the Lacaune breed and nine sheep from the Merino d'Arles breed (Online Resource 1). The Lacaune sheep come from seven different farms in southern France (Aveyron). They constitute four groups born in summer (26 July–11 August, N=5), early autumn (15–23 October, N=8), late autumn (1–5 December, N=6), and early winter (1 and 10 January, N=2) in different years (2013–2016). The Merino d'Arles sheep come from an experimental farm in southern France (Domaine du Merle, Salon de Provence) and were born in late summer/early autumn (12 September–10 October) or winter/early spring (25 February–7 April). All sheep were females aged between 2.5 and 5 years at time of slaughter (except one aged 6.5 years). This age class was targeted to provide third molars with fully developed crowns and limited tooth wear, more likely to deliver a complete record of an annual cycle.

The Lacaune and Merino sheep mandibles were recovered from the slaughterhouse with the sheep's identification buckles. The Merino sheep mandibles were dissociated from their respective buckles during processing at the slaughterhouse.

For this reason, the sheep can be attributed to a group born between late February and early April, or a group born in September/October but identification at the individual level could not be done (see Results and Discussion).

The third molars were extracted from mandibular bones and cleaned by boiling. Sequential sampling of enamel was performed by drilling series of bands perpendicular to the tooth growth axis, on the second lobe of the molar, and on the vestibular side. Each sample is located in tooth crown using its distance from the enamel-root junction (erj) (Balasse et al., 2003). The stable oxygen isotope ratios ($\delta^{18}O$) were measured on the carbonate fraction of enamel bioapatite. Enamel samples weighing ~ 600 µg were reacted with 100% phosphoric acid at 70 °C in individual vessels in an automated cryogenic distillation system (Kiel IV device), interfaced with a DeltaVAdvantage isotope ratio mass spectrometer. The analytical precision for each run, estimated from 6 to 8 analyses of our laboratory carbonate standard (Marbre LM, expected value − 1.83‰ calibrated to the NBS 19 international standard) is lower than 0.05‰.

The retrieved intra-tooth sequences of stable oxygen isotope ratios reflect the recording of the seasonal cycle during tooth crown formation (Bryant et al., 1996a, b), spanning approximately a year in the sheep third molar (Weinreb & Sharav, 1964; Milhaud & Nezit, 1991). Stable oxygen isotope ratios in the mineral fraction of animal skeletons linearly correlate to the stable oxygen isotope composition of local annual precipitation (Land et al., 1980; D'Angela & Longinelli, 1990). In continental Europe, the precipitation $\delta^{18}O$ values are affected by seasonal variations in air temperature, resulting in cyclical variations on an annual scale (Rozanski et al., 1993). Additionally, a significant part of seasonal variation in body water oxygen isotope composition results from animal behavior and physiology in response to changes in temperature and air humidity (Chen et al., 2017). All factors combine to create a seasonal signal in tooth enamel $\delta^{18}O$ values. As the tooth growth timing is fixed within species, the season of birth determines the sequence of the annual cycle recorded in a given tooth.

The $\delta^{18}O$ sequences measured in the sheep M3 were modeled using an equation derived from a cosine function (the procedure is described in Balasse et al., 2012; see also Online Resource 2). The model defines the amplitude (A) and the mean (M) of the signal, as well as the position (x_0) of the maximum $\delta^{18}O$ value and the period of the cycle (X, distance over which the isotopic record covers one annual cycle). The latter is used to normalize the distances in order to eliminate inter-individual variability in tooth size. The resulting x_0/X ratio for each specimen is a reference value for the specimen's birth date. In addition to the $\delta^{18}O$ sequences obtained from the Lacaune and Merinos sheep molars, the previously published sequences from four North-Ronaldsay sheep born in April/May (Balasse et al., 2005) were also modeled. The x_0/X ratios are reported on circular charts reflecting the cyclical nature of seasonality (Balasse et al., 2020; see Online Resource 2 for the construction of this chart). All calculations have been carried out using the Microsoft Excel software. The fitting of the model to the dataset is estimated using the Pearson correlation coefficient (r) (Pearson function in the Excel software). We consider that the model describes adequately the dataset when $r \geq 0.91$.

Ram Effect Experimental Design

The experiments were conducted on Lacaune dairy sheep raised at the INRAE La Fage experimental domain (Aveyron, southern France). The Lacaune breed is a local breed whose place of origin is the southern Massif Central. The breed selection for characteristics linked to dairy production (milk quantity and richness, udder morphology) was done in Lacaune pure breed, only began recently (less than 50 years ago) and did not involve introgression of foreign genes (Barillet et al., 2016). The Lacaune dairy breed has never been selected on the ability for out-of-season lambing.

Experiment 1

The objective was to (i) determine whether Lacaune ewes in the continuous presence of rams (PR) ovulate spontaneously in the spring and, if so, in what proportions; (2) measure the effectiveness of a "ram effect" (RE) in spring in terms of ovulation, without previous stimulation of the ram (*i.e.*, without artificial excitation of sexual activity). Two groups of 20 ewes each were constituted on February 17, 2020 (day 0). The groups were balanced in age and weight and all were non-lactating ewes (Online Resource 3). The two groups were kept separately in different sheepfolds. In group PR (presence of ram), two rams were introduced on day 0 and were kept permanently with the ewes until the end of the experiment. In group RE (ram effect), the ewes were kept separated from rams until two rams were introduced into the group on May 18, 2020. Blood samples were taken from the jugular vein from May 11, twice a week until June 19 when the experiment finished.

Experiment 2

The relative proportion of ewes ovulating spontaneously in spring was determined in a sample of 100 lactating ewes. The group, which was representative of the flock, was composed of 31 ewes in first lactation (L1), 25 in L2, 14 in L3, and 30 in L4 or more. They were herded normally with the rest of the flock (450 ewes, *i.e.*, 550 in total) and kept separated from rams. Blood samples were taken from the jugular vein on May 3, May 6, and May 10, 2021.

In both experiments, ovulations were detected by measuring plasma progesterone (P4) concentrations. Blood samples were obtained by jugular venipuncture in 5 mL tubes containing heparin. Plasma was obtained after 30 min of centrifugation at $3{,}500 \times g$ and concentration of plasma progesterone was determined in samples using an immunoenzymatic assay as described previously (Canépa et al., 2008). Sensitivity of this assay was 0.25 ng/mL. The mean intra-assay and inter-assay coefficients of variation were $< 10\%$. Females with progesterone concentrations ≥ 1.0 ng/mL samples were considered to have ovulated (Thimonier, 2000).

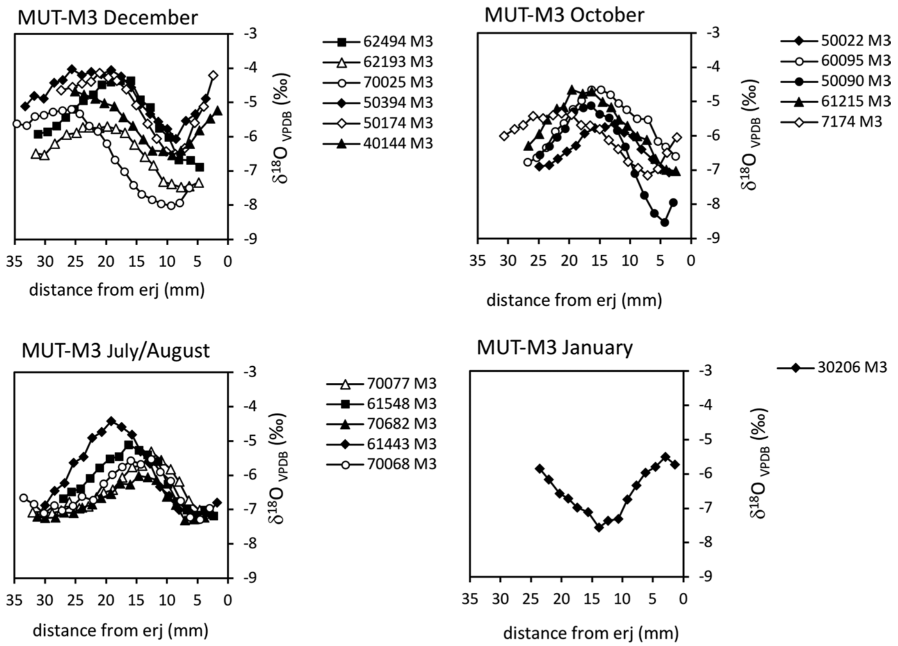
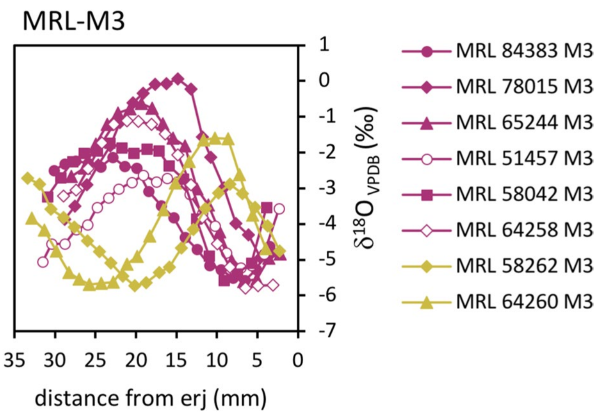


Fig. 1 Results from sequential analysis of stable oxygen isotope ratios in the Lacaune sheep tooth enamel. The sequences that could not be modeled are not included in this figure

Fig. 2 Results from sequential analysis of stable oxygen isotope ratios in the Merino sheep tooth enamel. The purple sequences are attributed to the autumn births group (September or October); the yellow sequences to the winter/early spring births group (late February, March, or early April)



Results from Stable Isotope Analysis of Sheep Enamel

Results from the sequential analysis of enamel stable oxygen isotope ratios and the modeling of the sequences are extensively reported in Online Resource 2. A large majority of $\delta^{18}O$ sequences show the expected pattern of cyclical variation reflecting the seasonal pattern (Figs. 1 and 2). Four of the 21 sequences obtained from the Lacaune sheep molars (MUT 161641–40131, MUT 161641–50136, MUT

161641–6119, and MUT 161345–50393) and one of the nine sequences obtained from the Merino sheep (MRL 84379) gave non-sinusoidal, strongly asymmetric, or incomplete annual $\delta^{18}O$ sequences and for this reason could not be modeled using the equation derived from a cosine function.

Among the Lacaune sheep, the mean x_0/X ratios for each birth group follow each other according to their respective place in the calendar cycle (Table 2). Within each birth group, the (x_0/X) ratios do not always rank according to the date of birth. Moreover, the reconstructed birth interval (in days) within each group is always higher than the real birth interval: although the Lacaune summer (July–August), early autumn (October), and late autumn (December) sheep were born respectively over 16, 10, and 5 days (in different years), the reconstructed birth interval is respectively 51, 53, and 57 days (Table 2). The x_0/X ratios of the Lacaune sheep born in October largely overlap with those born in August and partially with those born in December (Fig. 3a). The x_0/X ratios obtained from the Merino sheep were divided into two groups (Fig. 3b): in agreement with the pool of birth dates associated with these mandibles and from comparison with pre-existing references, six are attributed to September/October births and two to winter/early spring births. The mean x_0/X ratio measured for the Merino sheep born in Sept/Oct (0.69) is similar to the one measured for the Lacaune sheep born in October (0.67).

Results from the Ram Effect Experiment on Lacaune Ewes

Results from the ram effect experiment are given in Online Resource 3, Table 3, and Fig. 4. In both experiments, the percentage of spontaneously cycling ewes without ram is between 16 and 25%, and there is no difference between groups 2020-RE (before ram effect) and 2021-NR. In 2020 in non-lactating ewes, only 5 out of 20 ewes cycled in the group isolated from rams, and 6 out of 20 cycled in the group in permanent presence of rams. In 2021, among 100 lactating ewes maintained without rams, only 16 cycled.

In the 2020-RE group, the sudden introduction of rams in 2020 produced a dramatic increase in the number of ewes ovulating and this group of ewes showed 100%

Table 2 Mean and range of x_0/X ratios measured in the different birth groups in the Lacaune sheep (Δ = birth interval). Individual data are given in Online Resource 2

Reference sheep	Birth group (*N*)	Dates	Real Δ (days)	x_0/X (mean)	x_0/X (range)	Reconstructed Δ (days)
Lacaune	January (1)	10 Jan	/	0.05	/	/
	July–August (5)	26 Jul–11 Aug	16	0.62	0.14	51
	October (5)	15–23 Oct	10	0.67	0.15	53
	December (*N* = 6)	01–05 Dec	5	0.83	0.13	47

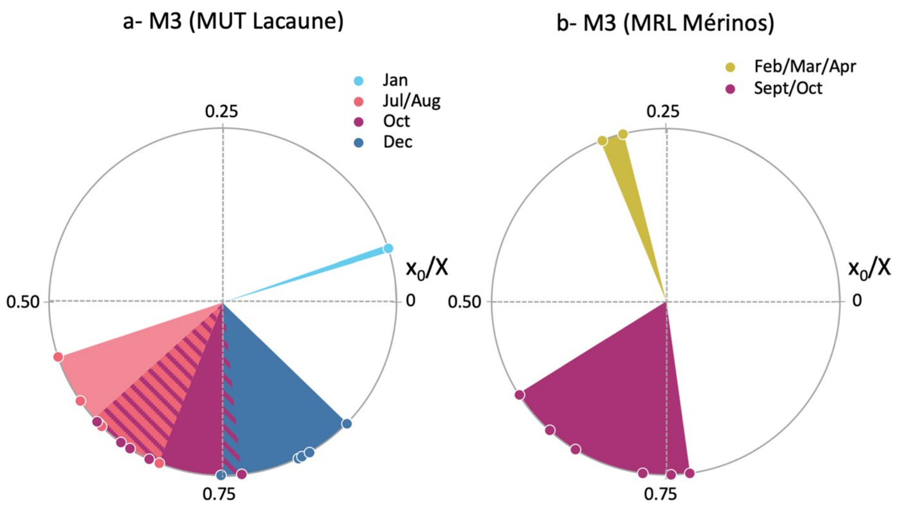


Fig. 3 Circular charts showing the distribution of x_0/X ratios calculated after the modeling of the $\delta^{18}O$ sequences measured in the Lacaune (**a**) and Merino sheep molars (**b**)

Table 3 Number of spontaneously cycling ewes, not cycling ewes, and cycling ewes after ram introduction, in each experimental set

	N ewes	Spont. cycling ewes	Non cycling ewes	Cycling ewes after ram introduction	*N* cycling ewes (total period)
2020-RE (ram effect)	20	5	15	15	20
2020-PR (presence of ram)	20	6	14	8	8
Fisher's exact test		NS		$P<0.01$	$P<0.01$
2021-NR (no ram)	100	16	84	/	16

of females cycling afterwards. At reverse, over the same period, in the 2020-PR group maintained in the permanent presence of rams, only 2 more ewes cycled.

Discussion

Interindividual Variability in the Recording of the $\delta^{18}O$ Sequences

Birth intervals appearing larger than they actually are, and the overlap in data between different birth groups are mostly due to inter-individual variability in the timing of tooth development: the sequence of the seasonal cycle recorded in a given tooth depends on when, during the annual cycle, the record began, *i.e.*, the date of birth (which we are trying to reconstruct) and the age at which the tooth began to form. The normalization procedure using the period of the cycle (X) eliminates

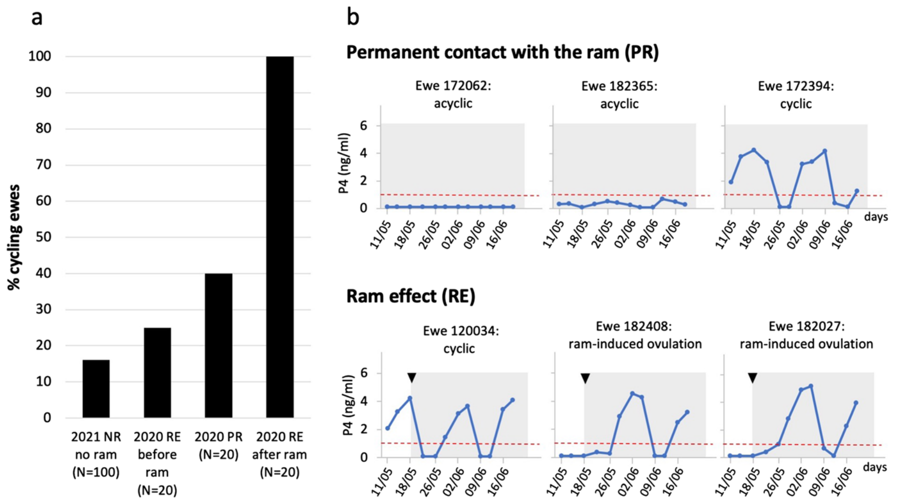


Fig. 4 **a** Percentage of cycling ewes in each experimental set. PR, presence of ram; RE, ram effect; NR, no ram. **b** Examples of variations in the concentration of plasma progesterone (P4) over the course of the experiment. The red dotted line sets the minimum progesterone concentration (1.0 ng/mL) at which ewes were considered to have ovulated. The black arrow indicates the date of introduction of the ram in the RE group. The shaded area indicates when the rams were present in the groups

variability in tooth size, not variability in the timing of tooth development. The latter has not been quantified in sheep molars, and the absence of a significant effect of sex, nutritional regime, and breeding age in cheek teeth eruption (Worley et al., 2016) does not mean the absence of inter-individual variability. From the results obtained in the Lacaune ewes born within five days in December, it appears that inter-individual variability in the timing of development of the third molar would have be approximately 1.5 months in this group. This methodological barrier must be taken into account when interpreting archaeological datasets.

Comparison with Preexisting Reference Sets for Sheep Birth Season

This new dataset from Lacaune and Merino sheep is combined to previous reference sets in Fig. 5. There is a good coherence between all reference sets in spite of the use of different sheep breeds, suggesting that interbreed variability in the timing of tooth development does not create significant additional imprecision for the determination of birth season. In the present state, this composite reference set allows to distinguish winter from spring births (notwithstanding a small overlap), and to distinguish both from mid-summer and autumn births. However, in the present state, it is not possible to distinguish mid-summer births from early autumn births (Fig. 5).

It should also be noted that different degrees of certainty are attached to these different reference sets. The highest degree of certainty may be given to the Lacaune reference sheep teeth, which all come from identified individuals with

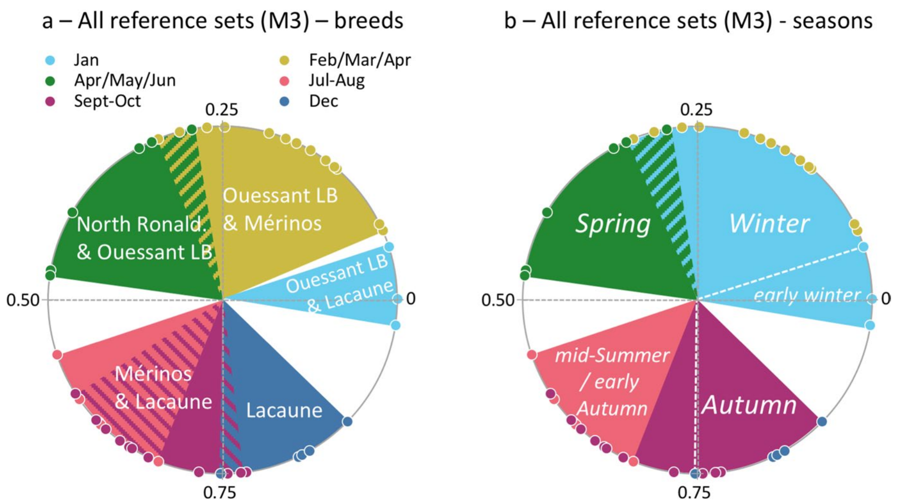


Fig. 5 Circular charts showing the distribution of x_0/X ratios in all reference sheep: **a** according to the breed and birth month: Ouessant × Landes de Bretagne (Kemenez; Balasse et al., 2020), North-Ronaldsay (Balasse et al., 2005), Lacaune (La Fage, this study), and Merino (Le Merle, this study). Monthly grouping; **b** seasonal grouping

known birth dates. The Merino sheep from Le Merle, disconnected from their identification buckles, were provided with birth dates grouped in two lots (winter and early spring, or autumn) that were far enough apart in the annual cycle to be clearly identified from the results of the analyses (Fig. 3b). Even though interindividual variability in the timing of tooth growth is a source of uncertainty, we consider it highly unlikely that it will lead to the misattribution of a winter/early spring birth to an autumn birth—and vice versa; nevertheless, within each births' group, the sheep cannot be attributed to a date of even a month of birth. The Kemenez reference set (Balasse et al., 2020) is composed of teeth collected on the Kemenez island. They all come from a unique flock for which sheep births had been precisely referenced over seven previous years (2008–2013 and 2015, $N = 255$), with almost all births occurring between mid-January and mid-April (94%), a marked lambing peak (73%) in February and until mid-March, and rare births in May/June, August, and October. The results could be compared to the known distribution of births. Most of them almost certainly belong to mid-January to mid-April and most likely to February until mid-March. The attribution of two of them to respectively May/June and October has a lower degree of certainty. Last, the North-Ronaldsay reference set (Balasse et al., 2005) includes mandibles collected from skeletons on the shore of North-Ronaldsay island. They derive from the collectively managed flock, in which lambing occurs mostly in April and May, but the precise birth dates were not known. Despite these uncertainties of varying degrees, the current paucity of modern references for $\delta^{18}O$ sequences lead us not to eliminate them but to consider each of them with the necessary caution, until additional data are produced.

Seasonal Distribution of Births and Management of Sheep Reproduction

Our experiment has shown that without manipulation of socio-sexual relations within the herd, the proportion of spontaneously cyclic ewes in the spring is low (16% in lactating females, 25% in non-lactating females) when males are absent, even in a breed with a high capacity for out-of-season breeding such as the Lacaune. The proportion of spontaneously cyclic ewes in the spring tended to be higher (40% vs 16%, Table 3, last column) when the ewes were left in contact with the rams. However, currently in a seasonal system where rams are kept permanently with the ewes with no manipulation by the herder, lambs are born in late winter (February). They reach puberty and are fertilized in mid-autumn or winter (November–December) if their growth rate is sufficient, then lamb in March–April. After a lactation of at least 3 months, they are fertilized with adults in the next autumn (September) to lamb in February. Ewe lambs that were not fertilized in their first year (if feeding conditions during growth were poor) and ewes that have lost their lamb and stopped nursing can escape to this scheme and be fertilized in the spring to give birth in autumn. Those do not predominate in the flock but can represent a few tenth of percent (10–20%). In such a system, autumn births could indeed occur, but they will be few (Mauléon & Dauzier, 1965; Perret, 1986).

We have shown that a ram effect could be performed in the Lacaune breed using non-sexually stimulated males, and that in such case, the ram effect is highly efficient (100% of females ovulating after the ram effect). These results, as well as many others already published (Martin et al., 1986), demonstrate that the ram effect is a simple and efficient way to obtain a majority of births in autumn, even though many other factors affect the outcome of ovulations into lambings. It must be noted that when separating and then joining again both sexes, a ram effect is implemented, whether intentionally by the herder to produce induced ovulation among ewes, or not just by joining rams and ewes. In an out-of-season system, the herder must then decide when and how he would start the “deseasoning” in his flock: (a) one possibility is to shift lambing time starting with the ewe lambs by delaying their fertilizations until when they are approximately 15 months old (in May, if born in February), then once adults, the ewes will always be fertilized in May and give birth in October to ewe lambs that will mate in May; (b) another possibility is to shift lambing time in adults by delaying the September mating to the following May. In both cases (a and b), it is necessary to separate rams from ewes at some point and for some time, and when the herder puts the males back with the females in the spring, there is a ram effect, even though perhaps unintentional. The two systems (a and b) are quite subtle and undoubtedly risky if herd management (feeding conditions and separation of sexes) is not well conducted and cannot be easily conceivable in situations where flocks are at pasture and mixed with others at certain periods (estivation). In such a system, autumn births can predominate if the management is successful or only reach around 60% if management fails. In the latter case, if spring fertility is low, the herder must set up autumn mating as a “catch-up” mating, with the problems that this entails, notably spring births and the difficulty of putting these ewes back into the spring mating scheme afterwards.

Conclusions and Perspectives

The results from the present study double the currently available reference data for sheep birth season inferred from $\delta^{18}O$ sequences in the third molar. They provide the first robust reference set for late summer and autumn births. Interindividual variability in the timing of the third molar growth has been shown to induce imprecision in the determination of birth date. If interindividual variability was similar in ancient sheep, this may also affect the determination of the duration of the lambing period. The new reference sets from Lacaune and Merino ewes combine well with previous ones obtained in other sheep breeds, suggesting that interbreed variability in the timing of tooth growth does not create significant additional imprecision. In the present state, it is unrealistic to try and determine sheep birth season on a monthly scale. In spite of these restrictions, some of which could be addressed with a statistical approach; when the data is enlarged, we can confirm that spring lambing, resulting from a reproduction cycle driven mainly by the photoperiodic cycle (that is, environmental factors), can be clearly distinguished from autumn lambing, involving manipulation of ewe reproductive cycle by the herders. This question would be the subject of major interest at the moment, illustrating complex interactions between animal physiology, environmental constraints, and technical systems.

Concerning herd management, this study has shown, on the one hand, that in the Lacaune breed with a high capacity for out-of-season breeding, the proportion of spontaneously cyclic ewes in the spring is low in the absence of males and remains minor when the ewes are left in permanent contact with rams. On the other hand, we were able to implement a highly efficient male effect using non-sexually stimulated males, demonstrating that this practice could have been implemented by Neolithic herders, even if we do not know if ancient ewes had the same responsiveness as the modern ones. The occurrence of predominant autumn births in a flock necessarily means a capacity for out-of-season breeding in the ovine population as well as a manipulation of reproduction involving the separation of both sexes in the autumn followed by their reuniting in the spring, thus achieving a male effect, whether intentionally or not. The interpretation of archaeological data in terms of reproduction management lies on the estimation of the relative proportion of autumn births, as autumn birth may also occur, without a manipulation by the herder but only to a small proportion. Larger archaeological datasets must be produced to achieve this goal, and combining data obtained from the second and third molars must be considered in the future, now that we have modern references for both teeth.

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Data Availability Data generated in this study are included in this article and its supplementary information files.

Declarations

Ethics Approval The experiment on the Lacaune sheep received approval by the ethics committee on animal experimentation, science and health (SSA), no. 115. The decision to authorize the project is referenced as APAFIS#22807–2019110814002486.

Competing Interests The authors declare no competing interests.

References

Avdi, M., & Chemineau, P. (1998). Reproductive and productive performance in Chios ewes mated in spring or in autumn. *Reproduction Nutrition Développement, 38*, 551–558.

Avdi, M., Banos, G., Kouttos, A., Pampoukidou, A., Bodin, L., Chemineau, P. (2002). Genetic variability of spontaneous out-of-season ovulatory activity in Chios sheep. 7th World Congress on Genetics Applied to Livestock Production Montpellier 19–23 August, (pp. 756–768).

Balasse, M., & Tresset, A. (2007). Environmental constraints on reproductive activity of domestic sheep and cattle: What latitude for the herder? *Anthropozoologica, 42*(2), 71–88.

Balasse, M., Smith, A. B., Ambrose, S. H., & Leigh, S. R. (2003). Determining sheep birth seasonality by analysis of tooth enamel oxygen isotope ratios: The Late Stone Age site of Kasteelberg (South Africa). *Journal of Archaeological Science, 30*, 205–215.

Balasse, M., Tresset, A., Dobney, K., & Ambrose, S. H. (2005). The use of isotope ratios to test for seaweed eating in sheep. *Journal of Zoology, 266*, 283–291.

Blaise, E., & Balasse, M. (2011). Seasonality and season of birth of modern and late Neolithic sheep from southeastern France using tooth enamel δ18O analysis. *Journal of Archaeological Science, 38,* 3085–3093. https://doi.org/10.1016/j.jas.2011.07.007

Balasse, M., Obein, G., Ughetto-Monfrin, J., & Mainland, I. (2012). Investigating seasonality and season of birth in past herds: A reference set of sheep enamel stable oxygen isotope ratios. *Archaeometry, 54*(2), 349–368. https://doi.org/10.1111/j.1475-4754.2011.00624.x

Balasse, M., Tresset, A., Bălăşescu, A., Blaise, E., Tornero, C., Gandois, H., Fiorillo, D., Nyerges, É. Á., Frémondeau, D., Banffy, E., & Ivanova, M. (2017). Sheep birth distribution in past herds: A review for prehistoric Europe (6th to 3rd millennia BC). *Animal*. https://doi.org/10.1017/S1751731117001045

Balasse, M., Renault-Fabregon, L., Gandois, H., Fiorillo, D., Gorczyk, J., Bacvarov, K., & Ivanova, M. (2020). 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. *Journal of Archaeological Science, 118*, 105–139. https://doi.org/10.1016/j.jas.2020.105139

Barillet, F., Lagriffoul, G., Marnet, P. G., Larroque, H., Rupp, R., Portes, D., Bocquier, F., & Astruc, J. M. (2016). Objectifs de sélection et stratégie raisonnée de mise en œuvre à l'échelle des populations de brebis laitières françaises. *INRA Productions Animales, 29*(1), 19–40.

Brooke C. H., Ryder M. L. (1979). *Races ovines méditerranéennes en régression*. United Nations FAO.

Bryant, J. D., Froelich, P. N., Showers, W. J., & Genna, B. J. (1996a). A tale of two quarries: Biologic and taphonomic signatures in the oxygen isotope composition of tooth enamel phosphate from modern and Miocene equids. *Palaios, 11*, 397–408.

Bryant, J. D., Froelich, P. N., Showers, W. J., & Genna, B. J. (1996b). Biologic and climatic signals in the oxygen isotopic composition of Eocene-Oligocene equid enamel phosphate. *Palaeogeography, Palaeoclimatology, Palaeoecology, 126*, 75–90.

Canépa, S., Lainé, A. L., Bluteau, A., Fagu, C., Flon, C., & Monniaux, D. (2008). Validation d'une méthode immunoenzymatique pour le dosage de la progestérone dans le plasma des ovins et des bovins. *Cahiers Des Techniques De L'INRA, 64*, 19–30.

Chasles, M., Chesneau, D., Moussu, C., Delgadillo, J. A., Chemineau, P., & Keller, M. (2016). Sexually active bucks are efficient to stimulate female ovulatory activity during the anestrus season also under temperate latitudes. *Animal Reproduction Science, 168*, 86–89.

Chazin, H. (2021). Multi-season reproduction and pastoralist production strategies: New approaches to birth seasonality from the South Caucasus region. *Journal of Field Archaeology, 46*, 448–460.

Chemineau, P., Guillaume, D., Migaud, M., Thiéry, J. C., Pellicer-Rubio, M. T., Malpaux, B. (2008). Seasonality of reproduction in mammals: intimate regulatory mechanisms and practical implications. *Reproduction in Domestic Animals*, 43 (suppl 2), 40–47.

Chen, G., Schnyder, H., & Auerswald, K. (2017). Model explanation of the seasonal variation of $\delta^{18}O$ in cow (*Bos taurus*) hair under temperate conditions. *Scientific Reports, 7*, 320. https://doi.org/10.1038/s41598-017-00361-y

Ciuti, S., Pipia, A., Grignolio, S., Ghiandai, F., & Apollonio, M. (2009). Space use, habitat selection and activity patterns of female Sardinian mouflon (*Ovis orientalis musimon*) during the lambing season. *European Journal of Wildlife Research, 55*, 589–595.

D'Angela, D., & Longinelli, A. (1990). Oxygen isotopes in living mammal's bone phosphate: Further results. *Chemical Geology: Isotope Geoscience Section, 86*, 75–82.

Delgadillo, J. A., Flores, J. A., Véliz, F. G., Hernández, H. F., Duarte, G., Vielma, J., Poindron, P., Chemineau, P., & Malpaux, B. (2002). Induction of sexual activity in lactating anovulatory female goats using male goats treated only with artificially long days. *Journal of Animal Sciences, 80*(11), 2780–2786.

Fabre, M., Bréhard, S., Hanot, P., Fiorillo, D., Vaquer, J., Balasse, M. (2021). Nouvel éclairage sur les systèmes d'élevage ovins du Chasséen. Reproduction, alimentation et productions animales à Auriac, Carcassonne (Aude, France). In E. Nicoud, M. Balasse, Desclaux E. & Théry-Parisot I. (Eds), *Biodiversities, environments and societies since Prehistory: new markers and integrated approaches*. 41^es rencontres internationales d'archéologie et d'histoire – Nice Côte d'Azur (pp. 101–112). Editions APDCA.

Girard, L. (1983). Moyens employés avec succès, par M. Morel de Vindé, Membre de la Société d'Agriculture de Seine et Oise, pour obtenir, dans le temps le plus court possible, la fécondation du plus grand nombre des brebis portières d'un troupeau. *Ephémérides de la Société d'Agriculture du Département de l'Indre pour l'An 1813, Séance du 5 Septembre, VIII Cahier, Châteauroux, Département de l'Indre.* VII, 66–68.

Hadjisterkotis, E. S., & Bider, J. R. (1993). Reproduction of Cyprus mouflon *Ovis gmelini ophion* in captivity and in the wild. *International Zoo Yearbook, 32*, 125–131.

Hadjikoumis, A., Vigne, J.-D., Simmons, A., Guilaine, J., Fiorillo, D., & Balasse, M. (2018). Autumn/winter births in traditional and Pre-Pottery Neolithic caprine husbandry in Cyprus: evidence from ethnography and stable isotopes. *Journal of Anthropological Archaeology, 53*, 102–111. https://doi.org/10.1016/j.jaa.2018.12.001

Hafez, E. S. E. (1952). Studies on the breeding season and reproduction of the ewe. Part I. The breeding season in different environments. Part II. The breeding season in one locality. *Journal of Agricultural Science, 42*, 189–231.

Hanocq, E., Bodin, L., Thimonier, J., Teyssier, J., Malpaux, B., & Chemineau, P. (1999). Genetic parameters of spontaneous spring ovulatory activity in Mérinos d'Arles sheep. *Genetics Selection Evolution, 31*(1), 77–90.

Hermes, T. R., Schmid, C., Tabaldiev, K., & Motuzaite Matuzeviciute, G. (2022). Carbon and oxygen stable isotopic evidence for diverse sheep and goat husbandry strategies amid a Final Bronze Age farming milieu in the Kyrgyz Tian Shan. *International Journal of Osteoarchaeology, 32*, 792–803.

Jones, H., Leigh, F. J., Mackay, I., Bower, M. A., Smith, L. M. J., Charles, M. P., Jones, G., Jones, M. K., Brown, T. A., & Powell, W. (2008). Population-based resequencing reveals that the flowering time

adaptation of cultivated barley originated east of the fertile crescent. *Molecular Biology and Evolution, 25*, 2211–2219. https://doi.org/10.1093/molbev/msn167
Karsch, F. J., Bittman, E. L., Foster, D. L., Goodman, R. L., Legan, S. J., & Robinson, J. E. (1984). Neuroendocrinal basis of seasonal reproduction. *Recent Progress in Hormone Research, 40*, 185–232.
Land, L. S., Lundelius, E. L., & Valastro, S. (1980). Isotopic ecology of deer bones. *Palaeogeography, Palaeoclimatology, Palaeoecology, 32*, 143–151.
Liu, X., Lister, D. L., Zhao, Z., Petrie, C. A., Zeng, X., Jones, P. J., Staff, R. A., Pokharia, A. K., Bates, J., Singh, R. N., Weber, S. A., Matuzeviciute, G. M., Dong, G., Li, H., LuÈ, H., Jiang, H., Wang, J., Ma, J., Tian, D., … Jones, M. K. (2017). Journey to the east: DIVERSE routes and variable flowering times for wheat and barley en route to prehistoric China. *PLoS ONE, 12*(11), e0187405. https://doi.org/10.1371/journal.pone.0187405
Malpaux, B., Viguié, C., Skinner, D. C., Thiéry, J. C., & Chemineau, P. (1997). Control of the circannual rhythm of reproduction by melatonin in the ewe. *Brain Research Bulletin, 44*, 431–438.
Martin, G. B., Oldham, C. M., Cognié, Y., & Pearce, D. T. (1986). The physiological-responses of anovulatory ewes to the introduction of rams - a review. *Livestock Production Science, 15*(3), 219–247.
Mauléon, P., & Dauzier, L. (1965). Variations de durée de l'anoestrus de lactation chez les brebis de race *Ile-de-France*. *Annales de Biologie Animale Biochimie Biophysique, 5*(I), 131–143.
Milhaud, G., & Nezit, J. (1991). Développement des molaires chez le mouton. Etude morphologique, radiographique et microdurométrique. *Recueil de Médecine vétérinaire, 167*(2), 121–127.
Perret, G. (1986). Races ovines. In ITOVIC Institut Technique de l'Elevage Ovin et Caprin (Ed. Paris) 441pp.
Peters, J., von den Driesch, A., & Helmer, D. (2005). The upper Euphrates-Tigris basin: cradle of agropastoralism? In J.-D. Vigne, J. Peters & D. Helmer (Eds) *First steps of animal domestication. New archaeozoological approaches*. *Proceedings of the 9th ICAZ Conference, Durham 2002* (pp. 96–124). Oxbow books.
Pfeffer, P. (1967). Le Mouflon de Corse (*Ovis ammon musimon* Schreber 1782); position systématique, écologie et éthologie comparées. *Mammalia, 31*(Suppl), 1–262.
Rendu C. 2003. *La montagne d'Enveig. Une estive pyrénéenne dans la longue durée*. Editions Trabucaire.
Rozanski, K., Araguas-Araguas, L., Gonfiantini, R. (1993). Isotopic patterns in modern global precipitation. In P. K. Stwart, K. C. Lohmann, J. McKenzie & S. Savin (Eds.), *Climate Change in Continental Isotope Records* (pp.1–36). American Geophysical Union
Sierra, A., Balasse, M., Rivals, F., Fiorillo, D., Utrilla, P., & Saña, M. (2021). Sheep husbandry in the early Neolithic of the Pyrenees: New data on feeding and reproduction in the cave of Chaves. *Journal of Archaeological Science: Reports, 37*, 102935. https://doi.org/10.1016/j.jasrep.2021.102935
Talibov, T. H., Weinberg, P. I., Mammadov, I. B., Mammadov, E. N., Talibov, S. T. (2009). Conservation strategy of the Asiatic mouflon (Ovis [orientalis] gmelini Blyth) and the Bezoar goat (Capra aegagrus Erxleben) in Azerbaijan. In Zazanashvili, N., Mallon, D. (Eds) *Status and protection of globally threatened species in the Caucasus* (p.46–52). CEPF Biodiversity Investments in the Caucasus Hotspot 2004–2009, Tiblisi.
Thiéry, J. C., Chemineau, P., Hernandez, X., Migaud, M., & Malpaux, B. (2002). Neuroendocrinal interactions and seasonality. *Domestic Animal Endocrinology, 23*, 87–100.
Thimonier, J. (2000). Progesterone level analysis for the determination of the physiological status of female farm animals. *Productions Animales, 13*(3), 177–183.
Todaro, M., Dattena, M., Acciaioli, A., Bonanno, A., Bruni, G., Caroprese, M., Mele, M., Sevi, A., & Trabalza Marinucci, M. (2015). Aseasonal sheep and goat milk production in the Mediterranean area: Physiological and technical insights. *Small Ruminant Research, 126*, 59–66.
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. *Journal of Archaeological Science, 40*, 4039–4055. https://doi.org/10.1016/j.jas.2013.05.013
Tornero, C., Balasse, M., Bălăşescu, A., Chataigner, C., Gasparyan, B., & Montoya, C. (2016a). The altitudinal mobility of wild sheep at the Epigravettian site of Kalavan 1 (Lesser Caucasus, Armenia): Evidence from a sequential isotopic analysis in tooth enamel. *Journal of Human Evolution, 97*, 27–36.
Tornero, C., Balasse, M., Molist, M., & Sana, M. (2016b). Seasonal reproductive patterns of early domestic sheep at Tell Halula (PPNB, Middle Euphrates Valley): Evidence from sequential oxygen isotope analyses of tooth enamel. *Journal of Archaeological Science: Reports, 6*, 810–818.

Tornero, C., Balasse, M., Bréhard, S., Carrère, I., Fiorillo, D., Guilaine, J., Vigne, J.-D., & Manen, C. (2020). Early evidence of sheep lambing de-seasoning in the Western Mediterranean in the sixth millennium BCE. *Scientific Reports, 10*, 12798. https://doi.org/10.1038/s41598-020-69576-w

Tresset, A., & Vigne, J.-D. (2011). Last hunter-gatherers and first farmers of Europe. *Comptes Rendus Biologies, 334*, 182–189.

Véliz, F. G., Moreno, S., Duarte, G., Vielma, J., Chemineau, P., Poindron, P., Malpaux, B., & Delgadillo, J. A. (2002). Male effect in seasonally anovulatory lactating goats depends on the presence of sexually active bucks, but not estrous females. *Animal Reproduction Sciences, 72*(3–4), 197–207.

Ventresca Miller, A. R., Harudae, A., Varfolomeev, V., Goryachev, A., & Makarewicz, C. A. (2020). Close management of sheep in ancient Central Asia: evidence for foddering, transhumance, and extended lambing seasons during the Bronze and Iron Ages. *STAR: Science & Technology of Archaeological Research., 6*, 41–60.

Weinreb, M. M., & Sharav, Y. (1964). Tooth development in sheep. *American Journal of Veterinary Research, 25*(107), 891–908.

Worley, F., Baker, P., Popkin, P., Hammon, A., & Payne, S. (2016). The Sheep Project (2): the effects of plane of nutrition, castration and the timing of first breeding in ewes on dental eruption and wear in unimproved Shetland sheep. *J Archaeol Sci: Rep, 6*, 862–874.

Zazzo, A., Balasse, M., Passey, B. H., Moloney, A. P., Monahan, F. J., & Schmidt, O. (2010). The isotope record of short−and long−term dietary changes in sheep tooth enamel: Implications for quantitative reconstruction of paleodiets. *Geochimica et Cosmochimica Acta, 74*, 3571–3586.

Zeder, M. A. (2008). Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. *Proceedings of the National Academy of Sciences, 105*, 11597–11604.

Zeder, M. A. (2015). Core questions in domestication research. *Proceedings of the National Academy of Sciences, 112*(11), 3191–3198.

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