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# Investigating the exploitation pattern of a newly established species, the case of the Late-Glacial roe deer (*Capreolus capreolus*) at La Fru (Savoie, France)

Anne Bridault<sup>1</sup> · Annelise Binois-Roman<sup>2</sup> · Dorothée G. Drucker<sup>3</sup> · Gilbert Pion<sup>4</sup>

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## Abstract

The Late-Glacial period offers a key window into the expansion of temperate species from southern refugia towards northern areas and the impact of faunal change on hunting strategies. In the Jura and in the Alps, the arrival of red deer and the withdrawal of reindeer are coeval with the warming of the GI-1e. Very little is known about roe deer, however. A high-resolution study of the rich archaeofauna from the Early Azilian occupation at the Northern Alpine site of La Fru provides data on the habitat and exploitation of roe deer. Roe deer populations were already established in the region in the early Bölling (~GI-1e), as is shown by the earliest radiocarbon date of roe deer bones (14.7–14.3 ky cal BP, 1σ). This is the earliest post-Last Glacial Maximum evidence of this species in northern France. The specimens from the site show the highest  $\delta^{15}\text{N}$  values among the deer species present in the areas. This is probably linked to the roe deer's selective foraging of highly nutritious vegetation already available in the open habitat at that time. Our zooarchaeological study shows that roe deer was a key resource at La Fru and was intensively hunted between May and September. The mortality profile indicates a “deliberate” targeting of inexperienced subadults and weaker older animals. These new data provide further evidence that there was both a reorganization of the animal environment and a reorientation of hunting on red deer and roe deer associated with the Early Azilian culture during the Bölling chronozone.

**Keywords** Ageing · Mortality profile · Seasonality · Stable isotopes · Early Azilian · GI1e

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✉ Anne Bridault  
anne.bridault@cnrs.fr

Annelise Binois-Roman  
Annelise.Roman-Binois@univ-paris1.fr

Dorothée G. Drucker  
dorothee.drucker@ifu.uni-tuebingen.de

- <sup>1</sup> CNRS, UMR 7041 ArScAn- Archéologies environnementales, Nanterre, France
- <sup>2</sup> Université de Paris 1 Panthéon-Sorbonne et UMR 7041 ArScAn- Archéologies environnementales, Paris, France
- <sup>3</sup> Senckenberg Centre for Human Evolution and Palaeoenvironment, HEP-University of Tübingen, Tübingen, Germany
- <sup>4</sup> Saint-Alban-Leyse, France

## Introduction

The Late-Glacial period (ca. 18–11.6 kyr cal BP) is a key period in the re-expansion of temperate species from the southern refugia they occupied during the last glacial phase. According to genetic data and fossil remains, roe deer (*Capreolus capreolus*) expanded from eastern and southwestern Europe refugia and colonized Western and Western-Central Europe during the Late-Glacial (Lorenzini and Lovari 2006; Sommer et Zachos 2009). A literature survey of indirect radiocarbon dates shows that the change in the roe deer's northern range was broadly coeval to the global warming GI-1 event (Sommer et al. 2009). However, reviews of the occurrence of roe deer are seldom based on direct radiocarbon dating of identified bones, but rather “obtained for other materials from the layer in which roe deer bone remains were found” (Sommer et al. 2009). It is necessary to work at a much finer scale, however, to build scenarios that account for the relative importance of local and global factors. This is highly relevant in the areas most strongly affected by the

Last Glacial Maximum (LGM), such as the Jura and north-western Alps. At the onset of the Late-Glacial, these regions were intensively reoccupied by human groups associated with the Magdalenian culture, whose subsistence relied on reindeer (*Rangifer tarandus*) hunting until the beginning of the 15th millennium cal BP or GS2a-GI-1e transition (e.g., Cupillard et al. 2015). The first post-LGM remains of red deer (*Cervus elaphus*) and elk (*Alces alces*) are dated to that period in these areas. Shortly after the arrival of these temperate cervid species, reindeer retreated from these regions (Bridault et al. 2000; Bridault and Chaix 2009; Cupillard et al. 2015). Throughout the Late-Glacial, the red deer home range consisted of open areas, as shown by multi-isotopic analysis of red deer remains from the archaeological sites of these regions (e.g., Drucker et al. 2011a). Coeval or slightly asynchronous with this faunal turnover is the appearance of new axial projectile points, one of the hallmarks of Early Azilian material culture (e.g., Naudinot et al. 2017).

What was the impact of such environmental change on prey selection and hunting strategies? Very little is known about hunting strategies, in fact, especially with regard to the exploitation of roe deer during this key phase, owing to the paucity of securely dated faunal assemblages. The abundant archaeofauna from the Early Azilian occupation at the Northern Alpine site of La Fru (Savoie) offers a unique opportunity to study the economic importance of this resource for the site-occupants via zooarchaeological analyses, to investigate the habitat of roe deer through stable isotope analyses, and to clarify its chronological position at the site by direct AMS dating. In line with the research carried out for several years on a regional scale (e.g., Bridault et al. 2000; Bridault and Chaix 2009; Cupillard et al. 2015; Drucker et al. 2003, 2008, 2011a, 2012), this paper contributes to the issue of hunter-gatherer adaptation in a context of rapid environmental reorganization and technical change.

## La Fru rock shelter: excavations and chrono-stratigraphy

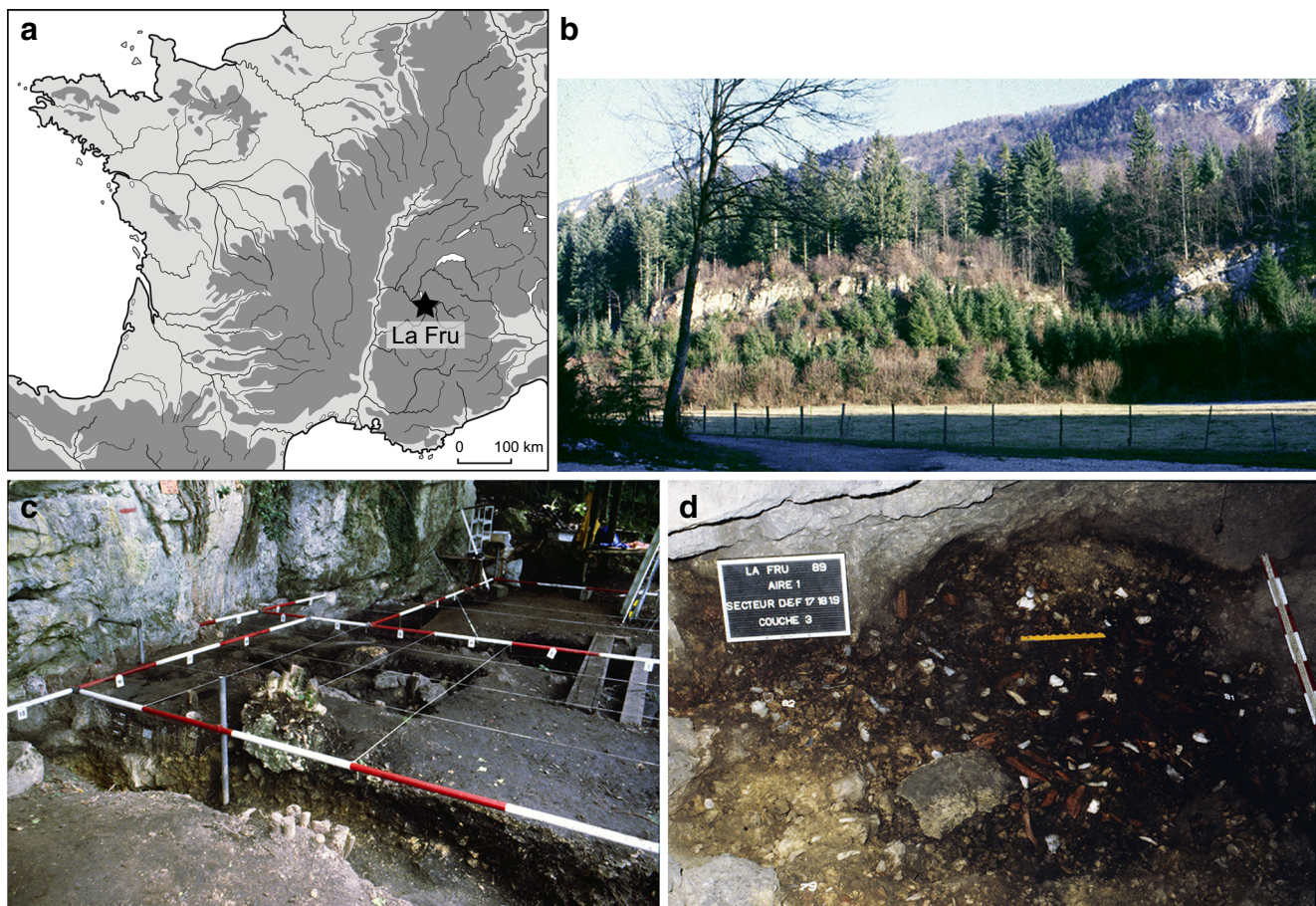
The site of La Fru has yielded some of the most significant Azilian and Mesolithic deposits found to date in the Northern Alps. It is an important site for the study of the post-LGM resettlement process and hunter-gatherer adaptation at the Late-Glacial/Holocene transition in the Northern Alps (Mevel 2013; Pion et al. 1990; Pion 1997, 2004, 2009). The La Fru rock shelter (45°27' N, 05°47'E) is located near the town of Chambéry, at the southern end of the Val de Couz (Savoie) (Fig. 1a, b). The latter, a natural corridor between the southern Jura, the Chartreuse mountains and the Vercors, has abundant, easily accessible siliceous resources that were exploited throughout the Late-Glacial (Bressy 2003). The site is located at 530 m asl on a promontory overlooking an

alluvial basin and at the base of a small Urgonian limestone cliff, 30 m high. Excavations by G. Pion (1981–1993) identified Magdalenian, Azilian and Mesolithic occupations across a strip approximately 100 m long and 3 to 4 m wide, divided into three Areas—I, II, and III—separated by huge boulders originating from the collapse of the ledge before the site was occupied (Pion et al. 1990). The manual excavation methods followed the current standards applied in prehistoric research: a grid with each square meter identified by a progressive letter and number (Fig. 1c), deposit layers progressively removed by successive arbitrary increments 2 to 3 cm thick (*décapages*), the use of scalpels and small brushes, and dry- and wet-sieving (1 mm) of the sediments. Artefacts and bones were partly recorded in three dimensions, partly by sieving bucket number.

The sedimentary deposits are 2.5 m thick in Area I, and seven lithostratigraphic horizons were identified: c1a- surface and c1b- Early Mesolithic, c2- Late Azilian, c3- Early Azilian and c4-A and B- Upper Magdalenian occupations, c5- stacked boulders resulting from the ledge collapse, c6- clay-rich horizon covering the bed-rock (Pion 2000). Early Azilian lithic material was also recovered in Layer 3 of Area II, approximately 40 m from Area I (Pion et al. 1990; Pion 2004).

In Area I, Layer 3 has an average thickness of 25 cm. Despite the precise excavation techniques employed, it was not possible to subdivide this layer into finer units based on the standard criteria of stratigraphy. Due to localized low sedimentation, Layer 2 transitions to Layer 3 without an intermediate level across part of the excavated surface. A difference in the colour (yellowish brown versus black) and texture of the sediments nevertheless enabled the two layers to be differentiated (Pion 1997, p. 320, Fig. 1d). Additionally, former clandestine excavations (denoted as “FC” among the artefacts and ecofacts) had disturbed a small volume of the Azilian layers in squares 22–25. Local issues of percolation along the cliff wall were observed on site and confirmed by palynological and anthracological studies (mentioned by Pion 1997, 2000, p. 151). The faunal remains were systematically collected over the entire excavated surface. All this material was initially attributed to the Early Azilian complex, including the batch from the disturbed area around the largest boulder, individualized as unit 1c. This batch was later reassigned to an undefined Azilian due to admixture found in the lithic industry. The first radiocarbon dates (conventional, except for one) were obtained from unidentified bone fragments from Level 3, Area I. The conventional dates yielded an age centered around on 11,800 BP, enabling the archaeologist to attribute this Early Azilian occupation to the beginning of the Allerød pollen zone (Pion 1997).

Given the importance of the sequence, complementary analyses—archeo-stratigraphy, lithic technology,



**Fig. 1** **a** Geographical location of the archaeological site of La Fru. **b** General view of the site (in the foreground). **c** View of Area I at the beginning of the excavations. **d** Detail of the excavation in Layer 3-Area 1 units D-E-F 17–19, with animal bones. Photos G. Pion

zooarchaeology, AMS radiocarbon dating, and stable isotopes on targeted species—have been performed starting in the 2000s as part of collective research programs<sup>1</sup>:

Four red deer bones from Layer 3-Area I and related undefined units were selected in order to date this cervid species. The resulting dates range from  $12,200 \pm 50$  BP (14.2–14 kyr cal BP,  $1\sigma$ ) to  $11,790 \pm 60$  BP (13.7–13.5 kyr cal BP,  $1\sigma$ ), corresponding to the Bölling and Alleröd chronozones. They were then all considered to be consistent with an Early Azilian cultural context (Oberlin and Pion 2009, p. 56). The extension of this archaeological culture until the beginning of the Alleröd chronozone is still considered valid (Naudinot et al. 2019, p. 29).

Detailed technological and stratigraphic revisions (vertical projections and conjoins) were undertaken by G. Pion and L. Mevel (Pion 2004; Mevel 2013), having identified artefacts from both Azilian technical traditions in Layer 3 of Area I (Pion 2004; Mevel and Bressy 2009). L. Mevel (Mével 2013) highlighted some post-depositional disturbances (12

conjoins out of 38 were found between the two Azilian layers 2 and 3 in squares 15–17), and a zone (E 19–23) where lithic artefacts from both Azilian occupations were found mixed (Mével 2013; Fig. 5). This same study (Mével 2013) considers all the published dates of Layer 3 (both conventional and AMS on deer bone) to chronologically define the Early Azilian culture. However, the correlation between direct dating on given species with the occurrence of a cultural phase based on lithic industry is perilous in this context and does not correspond to the scope of the investigation of the faunal guild turnover in response to environmental changes (e.g., Bridault et al. 2000; Bridault and Chaix 2009; Drucker et al., 2011a, b).

## Methods and materials

Although bones had been systematically collected over all of Area I, we chose to focus our zooarchaeological analysis on the subsample formed by square meters D-F/13–18, in order to avoid the area in which stratigraphic disturbances and admixture had been detected (Mével 2013). Due to the high bone content of the layer, this subsample was considered ample

<sup>1</sup> CNRS ECLIPSE “Cervus” project 2001–2003 (coord. A. Bridault) and a continuation of the PCR project “La fin du Paléolithique supérieur dans les Alpes du nord et le Jura méridional” 1997–2002 (coord. G. Pion).

enough to provide significant results. This was not, however, the case for dental remains: most of these were found discarded outside our selected area in a very dense dumping zone (Fig. 2), posing issues of sample representativity. We thus chose to consider all dental material from Level 3 in order to build the most representative mortality profile possible, at the risk of including some mixed elements.

Four roe deer bones from Layer 3 (three from the selected subsample of Area I and one from Area II) were then selected for AMS radiocarbon dating to establish the chronological position of the samples relatively to their stratigraphic attribution.

## Identification and quantification

An initial exploratory survey of the material was carried out by B. Caillat (in Pion et al. 1990, p. 111–112); our in-depth archaeozoological study reevaluated all animal remains from the selected areas. Our identifications (taxonomic and anatomical) and quantifications adhere to the conventional zooarchaeological techniques and terminology (e.g., Grayson 1984; Chaix and Méniel 1996). Taxonomic identification was carried out at the zooarchaeology laboratory of the Environmental Archaeology team in Nanterre, via the use of morphological and occasionally metrical criteria in comparison with reference collections and publications (Boessneck and Meyer-Lemppenau 1966; Bosold 1968; Bouvier 1966; Fernandez 2001; Grundbacher and Stampfli 1977; Helmer and Rocheteau 1994; Lemppenau 1964; Morel 1983; Morlat 2010; Pales and Garcia 1981; Pales and Lambert 1971; Rivals 2002; Wolff 1977). A total of 1807 (bones and teeth; no antler fragments) specimens were identified in squares D-F/13–18, to the species-level when possible, to the genus or group of species when it was difficult to discriminate between two or three closely related species, and by size class when it was impossible to achieve better accuracy. A further 468 dental

remains, retrieved from the remaining squares of Layer 3-Area I, were identified to species or genus.

Overall, bone surfaces are well preserved in the collection, with only a minimal number of remains showing significant degradation by post-depositional processes. The material is nonetheless highly fragmented, with an average weight of specimens identified to body part of only 2.56 g. In this assemblage of heavily fragmented remains, the presence of three small ruminants—roe deer, ibex and chamois—was a factor limiting specific identification. The post-cranial bones of these three species are indeed of similar size and morphology and are difficult to discriminate as osteological criteria are often applicable only to complete bone parts (Fernandez 2001). Another difficulty, associated with ibex, is that this species displays a significant osteometric sexual dimorphism, much higher than that observed among the other species in the faunal spectrum. The adult male is on average 50% taller than the female and can weigh more than three times as much. This results in females and youngsters appearing in the same size class as chamois and roe deer, while large males have bones that may have dimensions and robustness similar to those of wild boars and red deer. Unidentified ibex remains can therefore appear both among the small ruminants and the large artiodactyls. Because of these identification issues, a significant proportion of post-cranial remains was assigned to broad categories: unidentified small ruminant (roe deer, chamois and smaller ibexes), caprines (chamois and ibex), and unidentified large herbivores (red deer, wild boar, and large male ibexes).

## Determination of dental age at death

A total of 251 roe deer upper and lower jaw remains was retrieved from the excavated surface of Layer 3. Only the lower cheek teeth, the most abundant teeth in the assemblage, were included in the analysis of age-at-death distribution, as they are more appropriate for age estimation in ruminants (Payne 1973;

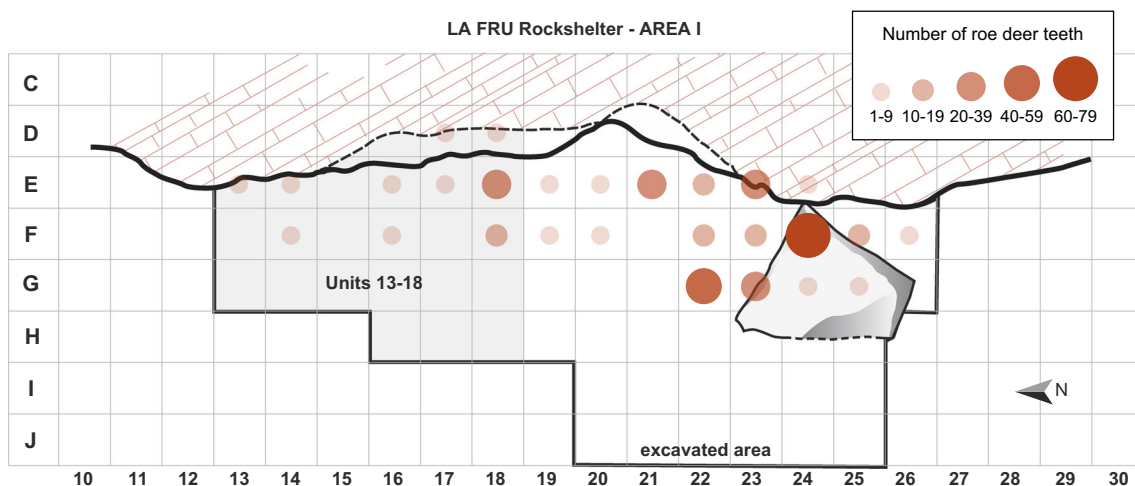


Fig. 2 Spatial distribution of roe deer dental remains in Layer 3-Area I, by number of teeth (CAD A. Binois-Roman and E. Magnifique-UMR 7041)

Brown and Chapman 1990,1991). These were macroscopically analysed with the help of published reference tables and the osteological collection of the zooarchaeology laboratory. We primarily employed the work of Tomé and Vigne (2003). They identify a maximum of 13 eruption, replacement and wear stages for mandibular teeth and illustrate a use-wear pattern for each tooth (d4, P3, P3, M1/M2, M3) by age stage. A scoring procedure allows assessment of the age-at-death range for specimens from birth up to dentally 140 months of age. The usefulness of this publication was however somewhat marred by the presence of editing errors in the tables published for the identification of use-wear stages. Indeed, in Table 2, presenting wear stages for the third premolar, the teeth illustrating stages 9 and 10 are P4s and not P3s (Tomé and Vigne, p. 162), whereas in Table 3 dealing with the fourth premolar, the teeth illustrating stages 8 and 9 are P3s and not P4s (Tomé and Vigne, p. 163). If the illustrations are switched, the corrected sequences appear to be missing a stage for the P3. Using the in-text descriptions of the use-wear stages and a reference collection of roe-deer mandibles of known age at death, we reconstructed the missing stage of the original paper, and publish here as Supplementary Materials 1 the two corrected tables in which the illustrations have been reordered and completed.

In addition, we also used the works of Carter (1997, 2001, 2006) to improve the accuracy of the estimation of the age of young animals. Based on radiographs of the lower jaws of roe deer, Carter identifies ten distinct stages of cheek tooth development coupled with a scoring system to assess the age-at-death range for dentally immature specimens up to 15–16 months. Stages 5 through 10, dealing with cheek teeth development from crown formation to root completion, were particularly useful to us in refining the age-at-death estimation of archaeological specimens, as the bodies of the jawbones were often fractured allowing direct observation of the stage of crown and root development in unerupted or erupting teeth.

In practice, we recorded tooth formation, eruption, and wear pattern stages for each lower cheek tooth present on the mandibular remains (except for the second premolar) and assigned them a score following the systems outlined above. The combination of premolar and molar scores then provided an estimated age for each mandible. The age estimation is most precise for fawns (0–6 months) and up to 12–14 months of age (maximum range 2–3 months); the more complete the dental rows, the more reliable and accurate is their estimated age. We then used these (sub-)complete dental rows as a reference standard for specific age groups in the studied sample, in order to assign ages to the least complete jaws and to isolated teeth. This allowed us to provide approximate age-at-death ranges for dental remains that could not have been included in the study otherwise; naturally, these ranges are much wider than those of complete mandibles, especially when the teeth are worn.

We also attempted to refit isolated lower teeth with mandible fragments as much as possible, and to match left and right

lower elements of the same age ranges, based on idiosyncratic patterns of wear, to reduce double counting and provide the best estimate of the minimum number of individuals. Only a few refittings of dental remains were achieved and no pairing (left and right mandibles) was identified, indicating that most dental remains pertain to a unique individual, and that each individual in the assemblage is represented by few dental elements (from a half-jaw to one tooth).

### Stable isotope analysis

We selected seven roe deer bones from La Fru, including three of the four directly dated remains, mostly originating from Layer 3 in Area I (Table 1). We added a red deer bone from Layer 3 to complete the existing data set for this species and the reindeer (*Rangifer tarandus*) from the western Alps, French Jura, and Swiss Jura during the GI-1e (Drucker et al. 2008, 2009, 2011a).

Collagen extraction was conducted at the Department of Geosciences of Tübingen University following the protocol of Longin (1971) as modified by Bocherens et al. (1997). In brief, the extraction procedure includes a step of demineralization in HCl 1 M, soaking in 0.125 M NaOH, and a solubilization in acidified water (pH = 2) before the freeze-drying process. The elemental analyses ( $C_{\text{coll}}$ ,  $N_{\text{coll}}$ ) and isotopic measurements ( $\delta^{13}C_{\text{coll}}$ ,  $\delta^{15}N_{\text{coll}}$ ) were performed in duplicate at the Institut de Ciències de l'Espai (ICTA-UAB) using a Thermo Flash 1112 (Thermo Scientific) elemental analyzer coupled to a Thermo Delta V Advantage mass spectrometer with a ConFlo III interface. This measures the ratios of  $^{13}C/^{12}C$  and  $^{15}N/^{14}N$  relative to a standard (V-PDB for carbon and AIR for nitrogen). The international laboratory standard IAEA 600 (caffeine) was used as well as two in-house reference materials (modern collagen of camel and elk). An analytical error below 0.2‰ (1 $\sigma$ ) was determined for  $\delta^{13}C$  and  $\delta^{15}N$  in all the repeated analyses. The reproducibility error for the amounts of C and N was lower than 2%. The biochemical reliability of the collagen was estimated by considering the chemical composition of collagen, with C/N atomic ratio ( $C:N_{\text{coll}}$ ) ranging from 2.9 to 3.6 (DeNiro 1985) and percentages of  $C_{\text{coll}}$  and  $N_{\text{coll}}$  above 8% and 3% respectively (Ambrose 1990). For radiocarbon dating, a  $C_{\text{coll}}$  content equal or above 30% is recommended (van Klinken 1999).

## Results and discussion

### The earliest dated evidence of roe deer populations during the Late-Glacial

The four dated roe deer samples (three from Area I, one from Area II) range between  $12,420 \pm 50$  BP and  $12,220 \pm 60$  BP, i.e., respectively 14.7–14.3 kyr cal BP 1 $\sigma$  and 14.2–14.0 kyr

**Table 1** Description of the selected reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*) samples from the site of La Fru and other sites of northeastern and southwestern France

Region	Site	Lab n°	Species	Sample	Excavation n°	Stratigraphy	Culture	NGRIP phase	Age BP	Age reference	14C source
French Jura	Rochedane	RCD500	Red deer	L radius	Ro70 D6 n° 19	D1	Final Magdalenian	GI-1e/1d	12,250 ± 70	GrA-21,512	Drucker et al. 2008
French Jura	Rochedane	RCD10900	Red deer	Metacarpal	A3	D1	Final Magdalenian	GI-1e/1d			
French Jura	Rochedane	RCD11000	Red deer	Metacarpal	A3	D1	Final Magdalenian	GI-1e/1d	12,230 ± 50	GrA-45,781	Drucker et al. 2011a
Switzerland	Champrévéryes	CHM-12	Red deer	Tibia	HrCh85 L13		Azilian	GI-1e			
Switzerland	Kesslerloch	KSL-45	Red deer	R calcaneus	M001:271	KESLM	Magdalenian	GI-1e	12,335 ± 45	KIA-33351	Napterala 2008
Western Alps	Les Douattes	LDT600	Red deer	Metatarsal	D99 F554	—	—	GS-2a/GI-1e			Drucker et al. 2008
Western Alps	La Fru	FRU-11	Red deer	L metacarpal	LF F24 885 c1c	Aire I, c1c	Early Azilian	GI-1e/1d	12,200 ± 50	GrA-34,354	Oberlin and Pion 2009
Western Alps	La Fru	FRU-30	Red deer	Metacarpal	LF F18 916	Aire I, c3	Early Azilian	GI-1e/1d	12,200 ± 50	Ly-14,438/SacA-50,817	This work
Western Alps	La Fru	FRU-5	Red deer	L talus	LF K70 1336-219	Aire III, c7	Magdalenian?	GI-1e/1d	12,260 ± 90	GrA-22,098	Drucker et al. 2008
Western Alps	Les Douattes	LDT300	Reindeer	Metapodial	F5-182	5 base	Magdalenian	GS-2a/GI-1e	12,255 ± 95	Ly-1416/OxA	Oberlin and Pion 2009
Western Alps	Campalou	ALP-17	Reindeer	Metatarsal		2	Azilian?	GI-1e	12,300 ± 60	Lyon-2301/OxA	Oberlin and Pion 2009
Western Alps	Le Tai	—	Reindeer	Bone	A3A4B3B4	Salle1, C"1	Azilian?	GS-2a/GI-1e	12,400 ± 60	Lyon-645/GrA-9714	Bridault et al. 2000
French Jura	Rochedane	RCD10800	Reindeer	Metapodial	Ro70 220 47/28	D1	Magdalenian	GS-2a/GI-1e	12,420 ± 75	Lyon-709/OxA-8030	Bridault et al. 2000
Western Alps	La Passagère	—	Reindeer	Bone		Néant	Magdalenian	GS-2a/GI-1e	12,440 ± 60	Lyon-641/GrA-9708	Bridault et al. 2000
French Jura	La Chênélaz	ALP-1	Reindeer	Phalanx II	M6 2975		Magdalenian	GS-2a/GI-1e	12,460 ± 65	Lyon-703/OxA-8027	Bridault et al. 2000
Western Alps	La Fru	FRU-19	Roe deer	Bone	LF J59 611	Aire II, c3	Magdalenian	GI-1e	12,250 ± 60	Ly-6169/SacA16267	This work
Western Alps	La Fru	FRU-31	Roe deer	Bone	D18 62 c3	Aire I, c3	Early Azilian	GI-1e	12,340 ± 50	Ly-9138/GrA	This work
Western Alps	La Fru	FRU-32	Roe deer	L calcaneum	E18 2658	Aire I, c3	Early Azilian	GI-1e			
Western Alps	La Fru	FRU-33	Roe deer	Metacarpal	E18 799 c3	Aire I, c3	Early Azilian	GI-1e			
Western Alps	La Fru	FRU-35	Roe deer	L metatarsal	E18 799 c3	Aire I, c3	Early Azilian	GI-1e			
Western Alps	La Fru	FRU-35	Roe deer	Metatarsal	F14 c3	Aire I, c3	Early Azilian	GI-1e			
Western Alps	La Fru	FRU-36	Roe deer	R metatarsal	E19 1087	Aire I, c3	Early Azilian	GI-1e	12,220 ± 60	Ly-9136/GrA	This work
Western Alps	La Fru	FRU-34	cf Roe deer	Metapodial	F14 890 c3	Aire I, c3	Early Azilian	GI-1e			

cal BP  $1\sigma$  (Table 2, Fig. 3). The earliest date ( $12,420 \pm 50$  BP) is, however, statistically different from the other three at a 95% confidence level ( $T = 8.298$  and  $\text{Chi}2(.05) = 7.8$  with 3DOF, Calib 7.0 software). Moreover, when all the dates from Level 3 are compared according to the same statistical tests, three groups of dates can be distinguished (see Table 2): one consists of the earliest roe deer date, which is the earliest obtained so far for Layer 3; a second group is composed of the three other roe deer dates and of five red deer dates (mean age =  $12,244 \pm 21$  BP, 14.2–14.1 kyr cal BP,  $1\sigma$ ), and the third group consists of three red deer samples from an ill-defined stratigraphic context (mean age =  $11,860 \pm 35$  BP, 13.6–13.7 kyr cal BP,  $1\sigma$ ). All dates are in the GI-1e (~Bölling), except for the more recent ones, which are in the GI-1c (~Alleröd) (see Table 2). It is very likely that the three dated remains of younger age stem from the overlying level (Late Azilian, Level 2) but found themselves mixed in Layer 3. Therefore, these dates should not be considered as associated to the Early Azilian context at the site. Finally, this chronological reappraisal supports the hypothesis that Level 3 of the La Fru rock-shelter corresponds to a palimpsest of a few successive occupation episodes fairly close together in time (Pion, 2004).

The other salient contribution of the dating results is that they provide the earliest dated evidence of the post-LGM presence of roe deer in eastern and northern France. The arrival of roe deer populations in the region in the first part of the GI-1e or at the GS-2a/GI-1e transition (if  $2\sigma$  error is considered, see Table 2) is thus coeval with that of red deer and elk (*Alces alces*) (Bridault and Chaix 2009). The remaining reindeer populations in the Northern Alps and Jura were still hunted in some places during this phase. According to the direct dates, the environment in this alpine area had a remarkable diversity of deer species between 15,000 cal BP and 14,000 cal BP (Supplementary Materials 2 and Table 2), up to the withdrawal of reindeer dated by 14,000 cal BP (Bridault et al. 2000; Oberlin and Pion 2009).

Published and unpublished AMS radiocarbon dates obtained from deer bones from southwestern France for the same period have been compiled for comparison purposes and are provided in Supplementary Materials 2. The early record of roe deer is a bone dated to 15,303–14,894 cal BP from the so-called brune-bigarrée layer at Moulin du Roc, a site located in the Dordogne (Jones 2006). Similar dates were obtained on red deer and reindeer bone samples from the same region and neighboring areas—Gironde, Landes, Pyrenees (Costamagno et al. 2016; Mallye et al. 2018; Szmidi et al. 2009). Thus, while roe deer were certainly present in the Dordogne during this period, namely Late GS-2a, it is difficult to establish their relative abundance in the environment. The low contribution of this species in the faunal spectrum at Moulin du Roc (NISP = 7, 2.7% NISP, Jones 2004: Table 6.2), suggests that it was a rare or little sought-after game.

Faunal turnover follows the same pattern in both regions, probably with a slight chronological lag. If we refer to the earliest dates, the expansion of temperate cervid species would have been somewhat (a few centuries) later in the Northern Alps than in southwestern France (Fig. 4). This seems plausible if one considers that the Southwest has never experienced continuous permafrost. The environment there was favorable to roe deer earlier than in northeastern France, where these conditions would have been achieved later. Stable isotope data shed significant light on this point (see below).

### Roe deer habitat in the northwestern Alps during the Late-Glacial

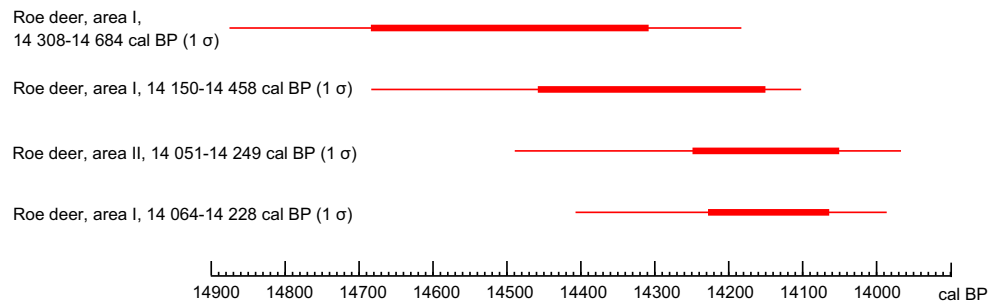
The  $\delta^{13}\text{C}_{\text{coll}}$  and  $\delta^{15}\text{N}_{\text{coll}}$  values of the roe deer of La Fru ranged from  $-21.8$  to  $-20.9\text{‰}$  and  $+3.3$  to  $+4.6\text{‰}$ , respectively (Table 3, Fig. 5a). The additional red deer from La Fru provided  $-21.1\text{‰}$  and  $+3.2\text{‰}$  as  $\delta^{13}\text{C}_{\text{coll}}$  and  $\delta^{15}\text{N}_{\text{coll}}$  values, which overlaps with the isotopic data of one sample of the roe deer group. However, the identification of this specific roe deer specimen was subject to caution (recorded as cf. *Capreolus capreolus*), since the remain was fragmentary, and could possibly belong to another species of small ruminant, such as chamois or female ibex. Pending biomolecular species identification by ZooMS, this specimen was removed from further analysis in this paper. The  $\delta^{15}\text{N}_{\text{coll}}$  values of the remaining roe deer appeared as the highest found among all deer, not only from the site of La Fru but also the western Alps, and the French and Swiss Jura regions ( $+0.8$  to  $+3.6\text{‰}$ ; Table 3, Fig. 5a). The roe deer  $\delta^{13}\text{C}_{\text{coll}}$  values were generally lower than those of the red deer and reindeer from these previously cited regions ( $-21.1$  to  $-19.2\text{‰}$  including the red deer of La Fru). An altitudinal effect would have resulted in higher  $\delta^{13}\text{C}_{\text{coll}}$  and lower  $\delta^{15}\text{N}_{\text{coll}}$  values in roe deer than in red deer, since La Fru is at higher altitude (ca. 570 m asl) than the sites from where red deer were analysed (ca. 355 to 450 m asl). We thus attribute the specific isotopic ratios of the roe deer to the use of a habitat different from those exploited by the other deer species. It was possible to consider published data from the same period, namely GI-1e, and from the same species found in three sites located in southwestern France (Gare de Couze, Moulin du Roc, Abri Faustin; Drucker et al. 2005, 2011b). Even if based on a smaller number of specimens, the reindeer, red deer and roe deer from southwestern France systematically exhibited higher  $\delta^{15}\text{N}_{\text{coll}}$  values ( $+3.0$  to  $+3.4\text{‰}$ ,  $+4.5$  to  $+5.3\text{‰}$ ,  $+4.7$  to  $+5.2\text{‰}$ , respectively) than their counterpart from northeastern France (Fig. 5b), reflecting the higher degree of soil maturity and vegetation development in more southern latitude (Drucker et al. 2012). Interestingly, red deer displayed  $\delta^{15}\text{N}_{\text{coll}}$  values as high as those of roe deer in southwestern France, but higher  $\delta^{13}\text{C}_{\text{coll}}$  values ( $-20.5$  to  $-19.7\text{‰}$  for red deer,  $-21.1$  to  $-20.8\text{‰}$  for roe deer). The sample size is still too limited to



**Table 2** Radiocarbon dating results for the faunal remains of Layer 3, attributed to the Early Azilian, and from an undefined Azilian context (1c and FC) in Area I. Radiocarbon calibrations are given with 1 and 2 sigma based on IntCal13 dataset (Reimer et al. 2013) and CALIB 7.1 software (Stuiver et al. 2019)

Area, level	Excavation #	Species	Anatomical part	Age BP	Lab. code	Cal BP, 1 sigma Intcal13 calib 7.0	Cal BP, 2 sigma Intcal13 calib 7.0	Pollen Chronozone	NGRIP stratigraphy	References
AMS										
Aire I, c3	LF E18 1839	Capreolus	Left scapula	12,420 ± 50	Ly-9137 (GrA)	14,308–14,684	14,875–14,183	Bölling	GI-1e	This work
Aire I, c3	LF D18 62	Capreolus	Left calcaneus	12,340 ± 50	Ly-9138 (GrA)	14,150–14,458	14,684–14,102	Bölling	GI-1e	This work
Aire II, c3	LF J59 611	Capreolus	Bone	12,250 ± 60	Ly-6169 (SacA 16,267)	14,051–14,249	14,489–13,967	Bölling	GI-1e	This work
Aire I, c3	LF F14 seuu 29	Capreolus	Metatarsal	12,220 ± 60	Ly-9136 (GrA)	14,023–14,199	14,393–13,920	Bölling	GI-1e	This work
Aire II, c3	LF K60 1163	Cervus	Bone	12,300 ± 70	Ly-6172 (SacA 16,270)	14,089–14,414	14,688–14,023	Bölling	GI-1e	This work
Aire III, c7	LF K70 1336	Cervus	Left talus	12,260 ± 90	GrA-22,098	14,015–14,382	14,717–13,914	Bölling	GI-1e/-1d	Drucker et al. 2011a
Aire I, c3	LF F24 885	Cervus	Left metacarpal	12,200 ± 50	GrA-34,354	14,018–14,160	14,260–13,934	Bölling	GI-1e/-1d	Oberlin and Pion 2009
Aire I, c3	LF F18 916	Cervus	Metacarpal	12,200 ± 50	Ly-14,438 (SacA-50,817)	14,018–14,160	14,260–13,934	Bölling	GI-1e/-1d	This Work
Aire I, c3	LF E24 360	Cervus	Phalanx	12,110 ± 110	Ly-134 (OxA 5264)	13,807–14,092	14,346–13,710	Bölling/Alleröd	GI-1e/-1c	Pion 1997
Aire I, c1c	LF F24 129 1c	Cervus	Average Left metacarpal	12,244 ± 21 11,950 ± 60	GrA-25,052	14,082–14,187 13,717–13,943	14,035–14,255 13,985–13,588	Bölling (ICBP) Older Dryas/Alleröd	GI-1d/-1c	Oberlin and Pion 2009
Aire I, FC	A9 QA0B FC 7	Cervus	Left metacarpal	11,840 ± 60	GrA-25,060	13,594–13,728	13,776–13,543	Alleröd	GI-1c	Oberlin and Pion 2009
Aire I, c1c	LF F25 386 1c	Cervus	Left metacarpal	11,790 ± 60	GrA-25,054	13,560–13,716	13,745–13,477	Alleröd	GI-1c	Oberlin and Pion 2009
Conventional			Average	11,860 ± 35		13,610–13,738	13,759–13,573	Alleröd		
Aire I, c3 bottom	F 15	Unidentified	Bone fragments	11,810 ± 160	Ly-2250			“Beginning of Alleröd”		Pion 1997
Aire I, c3 bottom	E 20	Unidentified	Bone fragments	11,820 ± 230	Ly-2408			“Beginning of Alleröd”		Pion 1997
Aire I, c3 heart	F 23	Unidentified	Bone fragments	11,740 ± 110	Ly-4325			“Beginning of Alleröd”		Pion 1997
Aire I, c3 upper	E 20	Unidentified	Bone fragments	11,680 ± 150	Ly-2409			“Beginning of Alleröd”		Pion 1997

**Fig. 3** AMS radiocarbon dates of the selected roe deer bones from La Fru

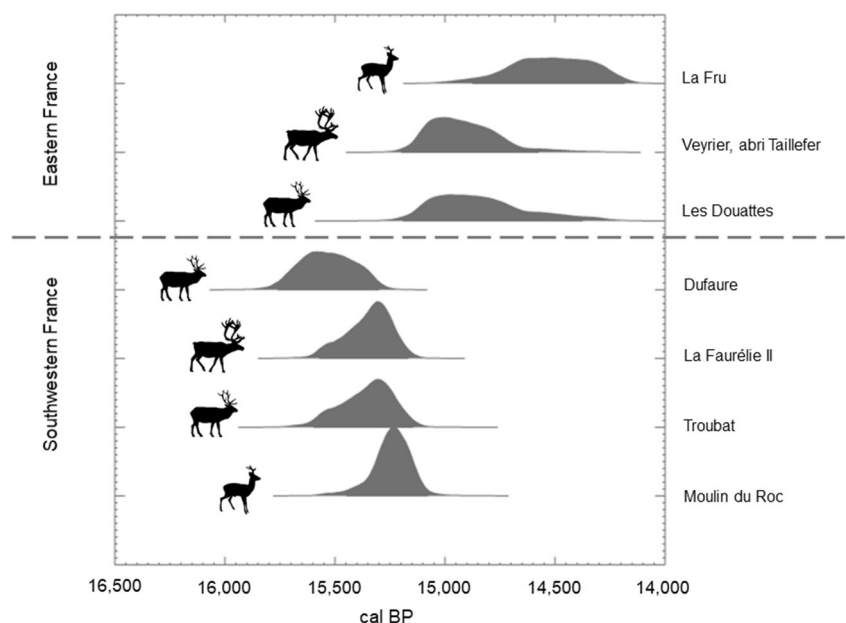


infer any conclusion on a strict niche partitioning between the two species in southwestern France. It is still noteworthy that the roe deer showed among the lowest  $\delta^{13}C_{coll}$  and highest  $\delta^{15}N_{coll}$  values among the deer guild.

With  $\delta^{13}C_{coll}$  values above  $-22\text{‰}$  for roe deer, red deer and reindeer, the habitat of the deer of the GI-1e at La Fru and the surrounding regions, as well as in southwestern France, clearly correspond to an open landscape with possibly scattered tree formations, in contrast to the dense temperate forest that developed later on. In the northwestern Alps at that time, there was extensive colonization of steppe grasslands by shrubs—*Hippophae*, *Juniperus*, and *Betula*—at low and medium altitudes in response to the intense global warming at the beginning of GI-1e. The presence of preserved *Betula* (*B. nana* and *B. pendula/pubscens*) macro remains in the Bölling infilling from la Thuile (Savoie, 884 m asl) confirms the local presence of birch stands at the beginning of this pollen zone (Bégeot et al. 2006). The impact of the slight climate degradation—Intra Bölling Cold Phase (IBCP)—interrupted birch expansion in favor of a slight increase in juniper and herbaceous taxa (ibid.). The Older Dryas cold event (ca 14.0–13.8 kyr cal BP) is recorded with a peak of pollen curves of *Betula* and *Salix* and a marked increase in

herbaceous values with altitude, reflecting an extension of steppe-like herbaceous vegetation. The expansion of pine forests up to 1000 m asl signals the onset of the Alleröd chronozone (ca 13.8–12.7 kyr cal BP). The decrease of light-demanding taxa can be related to denser forests at low altitude sites (Argant et al. 2009). Extant roe deer inhabit a wide variety of habitats, not only in deciduous, coniferous and Mediterranean forests but also in shrublands, moorlands and marshes (Tixier and Duncan 1996). The re-colonization of western Europe by roe deer could thus have pre-dated the expansion of dense temperate forest. Roe deer are generalist herbivores and concentrate feeders, which selectively consume plants or parts of plants with high nutritional quality (Hoffmann 1989; Duncan et al. 1998). The presence of roe deer at La Fru implies an advanced state of vegetation biomass (Tixier and Duncan 1996). The relatively high  $\delta^{15}N_{coll}$  values of the analysed roe deer are indeed consistent with the reflection of high soil maturity necessary to the development of highly nutritive vegetation (see Drucker et al. 2011a, 2012). The presence of local refuge regions, as suspected in the French Jura (Cupillard et al. 2015), may have contributed to early favourable conditions for roe deer in the hunting area of La Fru.

**Fig. 4** Roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and reindeer (*Rangifer tarandus*) calibrated dates (manufactured antler and bones excluded) from eastern and southwestern France at the GS-2a/GI-1e transition. Only the earliest radiocarbon dates for red deer and latest dates for reindeer are considered. Radiocarbon calibrations are based on IntCal13 dataset (Reimer et al. 2013) and CALIB 7.1 software (Stuiver et al. 2019)



**Table 3** Results of the elemental and isotopic analyses of the selected reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*) specimens from the site of La Fru and other sites of northeastern and southwestern France

Region	Site	Lab n°	Species	Sample	Excavation n°	Stratigraphy	Culture	Yield (mg/g)	C <sub>coll</sub> (%)	N <sub>coll</sub> (%)	C:N <sub>coll</sub>	δ13C <sub>coll</sub> (‰)	δ15N <sub>coll</sub> (‰)	NGRIP phase	Age BP	Age reference	*
French Jura	Rochedane	RCD500	Red deer	radius	Ro70 D6 n°19	D1	Final Magd.	30.0	42.3	15.5	3.2	-19.9	0.8	GI-1e/1d	12,250±70	GrA-21512	2
French Jura	Rochedane	RCD10900	Red deer	metacarpal	A3	D1	Final Magd.	61.8	41.7	16.0	3.0	-20.4	2.0	GI-1e/1d			
French Jura	Rochedane	RCD11000	Red deer	metacarpal	A3	D1	Final Magd.	50.3	44.0	16.1	3.2	-20.6	2.4	GI-1e/1d	12,230±50	GrA-45781	3
Switzerland	Champrevèyres	CHM-12	Red deer	tibia	HrCh85 L13		Azilian	21.9	38.0	14.0	3.2	-20.6	3.4	GI-1e			
Switzerland	Kesslerloch	KSL-45	Red deer	calcaneus	M001:271	KESLM	Magdalenian	141.8	44.4	15.4	3.4	-20.2	2.0	GI-1e	12,335±45	KIA-33351	5
Western Alps	Les Douaites	LDT600	Red deer	metatarsal	D99 F554	-		56.0	41.8	15.4	3.2	-19.8	2.0	GS-2a/GI-1e			2
Western Alps	La Fru	FRU-11	Red deer	metacarpal	LF F24 885 c1c	aire I. c1c	Early Azilian	76.2	41.5	15.7	3.1	-19.2	1.3	GI-1e/1d	12,200±50	GrA-34354	6
Western Alps	La Fru	FRU-30	Red deer	metacarpal	LF F18 916	aire I. c3	Early Azilian	-	37.8	13.3	3.3	-21.1	3.2	GI-1e/1d	12,200±50	Ly-14438	7
Western Alps	La Fru	FRU-5	Red deer	talus	LF K70 1336-219	aire III. c7	Magdalenian?	55.2	36.3	14.1	3.0	-20.3	3.6	GI-1e/1d	12,260±90	GrA-22098	2
Western Alps	Les Douaites	LDT300	Reindeer	metapodial	F5-182	5 base	Magdalenian	29.4	42.1	15.9	3.1	-19.9	1.7	GS-2a/GI-1e	12,255±95	Ly-1416/	6
Western Alps	Campalou	ALP-17	Reindeer	metatarsal		2	Azilian ?	28.3	37.7	14.4	3.1	-19.5	2.7	GI-1e	12,300±60	Lyom-2301/	6
Western Alps	Le Tai	-	Reindeer	bone	A3A4B3B4	salle1. C'1	Azilian ?	-	45.2	16.1	3.3	-20.2	1.8	GS-2a/GI-1e	12,400±60	Lyom-645/	1
French Jura	Rochedane	RCD10800	Reindeer	metapodial	Ro70 220 47/28	D1	Magdalenian	44.6	37.2	13.7	3.2	-20.3	2.1	GS-2a/GI-1e	12,420±75	Lyom-709/	1
Western Alps	La Passagère	-	Reindeer	bone		néant	Magdalenian	-	44.5	15.9	3.3	-19.8	1.4	GS-2a/GI-1e	12,440±60	Lyom-641/	1
French Jura	La Chênélaz	ALP-1	Reindeer	phalanx II	M6 2975	2	Magdalenian	37.2	38.1	14.5	3.1	-19.9	1.9	GS-2a/GI-1e	12,460±65	Lyom-703/	1
Western Alps	La Fru	FRU-19	Roe deer	bone	LF J59 611	aire II. c3		33.3	39.0	14.6	3.1	-21.0	3.9	GI-1e	12,250±60	Ly-6169/	7
Western Alps	La Fru	FRU-31	Roe deer	calcaneum	D18 62 c3	aire I. c3	Early Azilian	59.5	40.5	14.5	3.3	-20.9	3.8	GI-1e	12,340±50	Sac- A16267	7
Western Alps	La Fru	FRU-32	Roe deer	metacarpal	E18 2658	aire I. c3	Early Azilian	99.7	42.6	15.2	3.3	-21.4	4.1	GI-1e			
Western Alps	La Fru	FRU-33	Roe deer	metatarsal	E18 799 c3	aire I. c3	Early Azilian	56.1	38.0	13.5	3.3	-21.0	4.2	GI-1e			
Western Alps	La Fru	FRU-35	Roe deer	metatarsal	F14 c3	aire I. c3	Early Azilian	33.0	34.2	12.0	3.3	-21.6	4.6	GI-1e	12,220±60	Ly-9136/	7
Western Alps	La Fru	FRU-36	Roe deer	metatarsal	E19 1087	aire I. c3	Early Azilian	72.1	39.1	13.7	3.3	-21.8	4.5	GI-1e			
Western Alps	La Fru	FRU-34	Roe deer?	metapodial	F14 890 c3	aire I. c3	Early Azilian	55.5	38.7	13.6	3.3	-21.2	3.3	GI-1e			
Dordogne	Gare de Couze	GCZ-11	Red deer	calcaneum	Couze G0	G0 or G0-G0	Upper Magd.	22.8	32.7	11.4	3.4	-20.5	4.5	GI-1e			
Dordogne	Gare de Couze	GCZ-12	Red deer	mandible	Couze G0	G0	Upper Magd.	32.1	32.3	11.1	3.4	-20.1	5.3	GI-1e			
Dordogne	Gare de Couze	GCZ-10	Reindeer	humerus	Couze G0	G0 or G0-G0	Upper Magd.	17.5	34.8	11.9	3.4	-19.8	3.4	GI-1e			
Dordogne	Moulin du Roc	MRC-15	Red deer	phalanx	MDR05D41D#227	brune-bigarrée	Final Magd/	27.5	40.9	14.6	3.3	-19.7	5.2	GI-1e	12,260±60	GrA-48898	7
Dordogne	Gare de Couze	GCZ-9	Reindeer	humerus	Couze G0	G0	Upper Magd.	30.7	39.0	13.8	3.3	-20.0	3.0	GI-1e	12,490±50	GrA-43937	4

Table 3 (continued)

Region	Site	Lab n°	Species	Sample	Excavation n°	Stratigraphy	Culture	Yield (mg/g)	C <sub>coll</sub> (%)	N <sub>coll</sub> (%)	C:N <sub>coll</sub>	δ13C <sub>coll</sub> (‰)	δ15N <sub>coll</sub> (‰)	NGRIP phase	Age BP	Age reference	*
Gironde	Abri Faustin	AF1700	Roe deer	metatarsal			Upper Magd.	50.9	40.5	14.7	3.2	-20.8	4.9	GI-1e			
Gironde	Abri Faustin	AF1800	Roe deer	mandible	CSC		Upper Magd.	2.6	32.3	12.6	3.0	-20.8	4.7	GI-1e			
Dordogne	Moulin du Roc	MRC 12	Roe deer	phalanx II	MDR05E41D#294	brune-bigarrée	Final Magd.	49.3	39.3	13.6	3.4	-20.9	5.2	GI-1e/GI-1d			
Dordogne	Moulin du Roc	MRC 13	Roe deer	metapodial	MDR05E41A#11	brune-bigarrée	Final Magd.	94.3	40.8	14.3	3.3	-21.1	4.8	GI-1e/GI-1d			
Dordogne	Moulin du Roc	MRC 2	Roe deer	metatarsal	MDR05D41C#53	brune-bigarrée	Final Magd.	44.8	36.6	12.6	3.4	-20.8	4.7	GI-1e/GI-1d	12.170±50	GrA-44601	4

\*: Bibliographical reference of <sup>14</sup>C date : 1: Bridault et al. 2000; 2: Drucker et al. 2008; 3: Drucker et al. 2011a; 4: Drucker et al. 2011b; 5: Napierala 2008; 6: Oberlin and Pion 2009; 7: this work.

### Roe deer: a key resource at la Fru in Layer 3

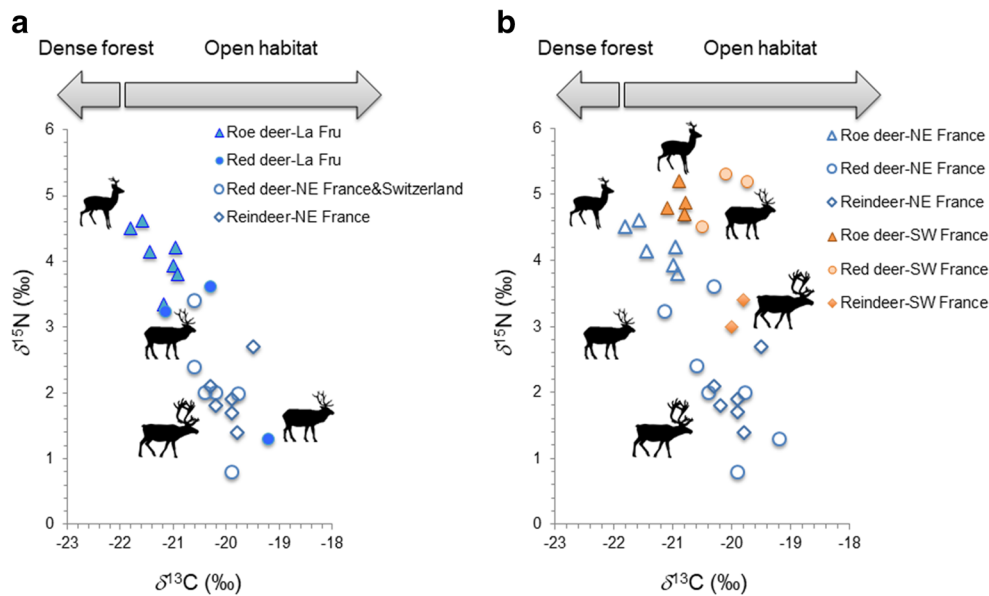
#### Structure of the faunal spectrum

The faunal spectrum highlights a high taxonomic richness with 13 mammalian taxa, including five ungulate species. Species distribution is here highly unusual, as the roe deer appears to be the first hunted species according to the dental remains (N 251 = 38.4%, Fig. 6) and is second only to red deer based on skeletal remains (NISP 301 = 16.7% of the total NISP, Fig. 7). The discrepancy between these two results is related to issues of identification: the highly fragmented skeletal remains of small ruminants were difficult to assign confidently to a given species, and many—of which many roe deer remains—were therefore recorded as “unidentified small ruminant.” Red deer remains, on the other hand, were more easily identified to species level. This leads to an underrepresentation of the roe deer relatively to the red deer in the skeletal remains. As such issues are not encountered with teeth, which are rarely fragmented in the assemblage and easily discriminated between artiodactyl species, the actual representation of the roe deer in Layer 3 is probably more accurately depicted in the dental spectrum. Ungulates account for 87.6% of the identified remains; interestingly, the frequencies of medium and large herbivores are similar (respectively 49.2% and 44.7% of the NISP).

The association of cervids with species of alpine and craggy environments such as chamois (*Rupicapra rupicapra*), ibex (*Capra ibex*), marmot (*Marmota marmota*), and hare (*Lepus timidus/europaeus*), is frequent at low and mid-altitude regional sites during the Late-Glacial (Bridault and Chaix 1999). The discreet contribution of marmot and hare contrasts with the abundance of the remains of these small game species in the Late-Glacial sites of the region located at a higher altitude (~1000 m asl), such as Les Freydières and Collomb (e.g. Bouchud 1956; Bouchud and Desbrosses 1973; Patou 1987). Finally, the studied assemblage is characterized by the diversity of wild carnivore species of all sizes: brown bear (*Ursus arctos*), wolf (*Canis lupus*), badger (*Meles meles*), red fox (*Vulpes vulpes*), marten (*Martes* sp.), and stoat (*Mustela erminea*).

#### Representation of the skeletal elements

The exploitation of the roe deer in the Early Azilian was investigated on remains from squares D-F/13–18 by the analysis of skeletal part distribution (detailed list available in Supplementary Materials 3) The resulting illustration (Fig. 8) must however be interpreted in light of the identification issues encountered with this material; notably, the apparent absence of the axial skeleton and of the pelvis are to be related with their high fragmentation and low morphologic specificity, preventing their identification at the species level.



**Fig. 5** **a** Stable isotope data of the selected reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*) specimens from the site of La Fru and surrounding regions. NE France stands for the French Jura and Western Alps. **b** Stable isotope data of reindeer (*Rangifer*

*tarandus*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*) from NE France (French Jura and Western Alps) and SW France (Dordogne and Gironde)

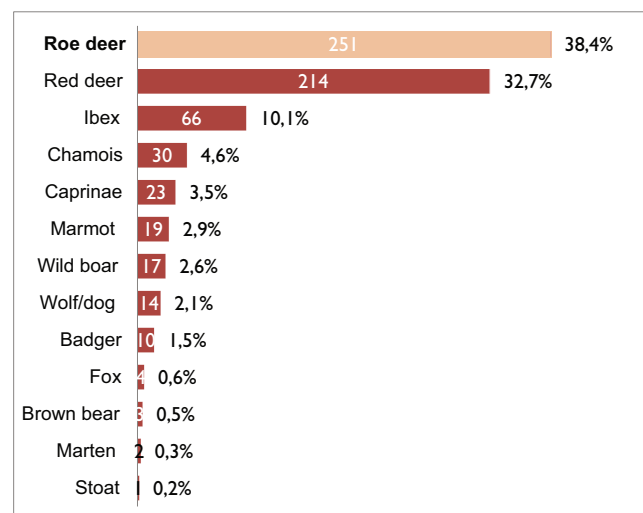
The distribution presented here is therefore slightly misleading, as all skeletal elements are in all likelihood present among the remains. It appears therefore that roe deer were mostly transported back to the site as complete carcasses; the slight over-representation of hind limb elements may convey occasional events of off-site primary butchering and selection of the meatier quarters.

### A targeted hunting strategy?

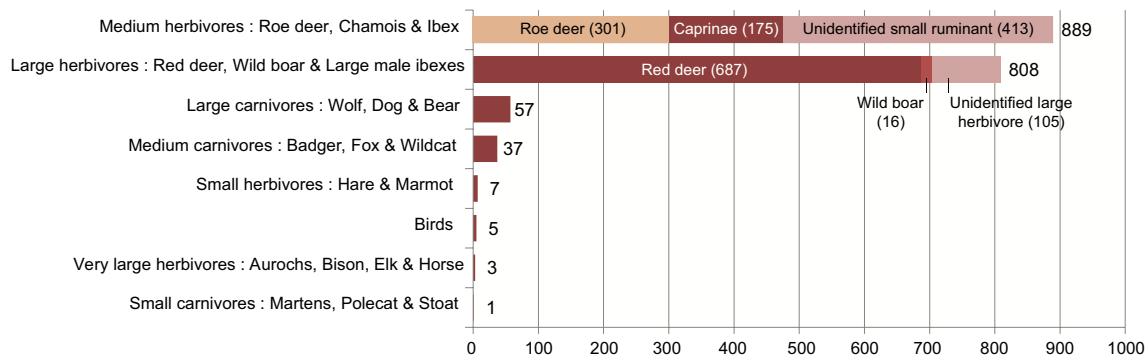
Age-at-death profiles were constructed from a sample of 176 lower cheek teeth representing a minimum of 94 different individuals (MNI) (detailed list available in Supplementary Materials 4), the largest roe deer sample to date for the Epipalaeolithic and Mesolithic periods in France. The dental remains are unevenly distributed into nine age classes ranging from 3 months to 9 years (Fig. 9). As these classes are of uneven span, the graphic visualization of age-class distribution weighs the number of teeth and individuals by age class width, with results expressed as “corrected numbers” (Table 4, Brochier 2013). The two age-at-death distributions, by number of teeth and number of individuals, are not statistically significant (Kolmogorov-Smirnov Test:  $D = 0.350$ ,  $p$  value = 0.078,  $\alpha = 0.05$ ). It appears that over a fourth of all individuals (26.1%, Fig. 10) died as subadults in between the ages of 12 and 18 months, a share of the population appearing unusually high for a span of only 6 months.

Did Early Azilian hunters target specific individuals among the roe deer population? Should roe deer hunting be

indiscriminate, it would be expected that the age-at-death profile would demonstrate a structure resembling that of a natural population. To allow this comparison, we reconstructed the age-class structure of a “natural” roe deer population based on the survivorship data published in Fruzinski and Labudzki (1982, p. 370: Table 4 and Fig. 1) obtained on a population of Polish forest roe deer submitted to regulated hunting. Mortality was highest in the first 6 months of life (37.6%);



**Fig. 6** Distribution of taxa in Layer 3-Area I (whole excavated surface) at La Fru, expressed as the frequency of number of dental remains (NISP, number of identified specimens) ( $N = 646$ , of which  $N = 183$  stem from units 13–18 and the remainder from units 19–26)



**Fig. 7** Distribution of taxa in Layer 3-Area I (units 13–18) at La Fru, expressed as frequency of NISP (number of identified specimens) ( $N = 1807$ , including dental remains ( $N = 183$ ) and antler fragments ( $N = 3$ ))

adults died mostly of human predation and of occasional harsh winter conditions. The average life-span was 2.9 years. We transformed the data from the published survivorship curve to the theoretical age structure of a live population at the 1st of June (i.e., at birth of the fawns) by calculating the percentage represented by each age class (see Supplementary Materials 5-table, column *lxp*) over the total population (Supplementary Materials 5-table, sum of column *lxp*). The resulting curve is presented in Supplementary Materials 5. Its comparison with the mortality data collected at La Fru highlights an under-representation of fawns at La Fru (ca - 46%), while subadults (+ 68%) and older adults (ca + 100%) are significantly over-represented; prime adults display similar proportions in both populations.

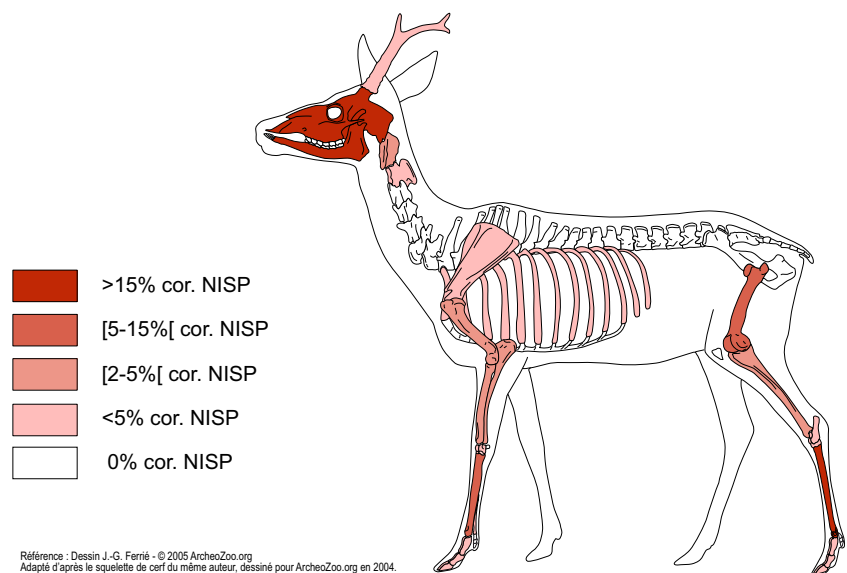
These results must be interpreted in light of the roe deer’s behavior and life cycle. After birth, roe deer fawns remain hidden in the vegetation for the first 4 weeks of the lactation period. They are at the time more likely to fall prey to predators such as fox or lynx (Jarnemo et al. 2004) than to humans. The absence of fawns under 3 months of age in the assemblage most likely reflects the fact that they escape the sight and

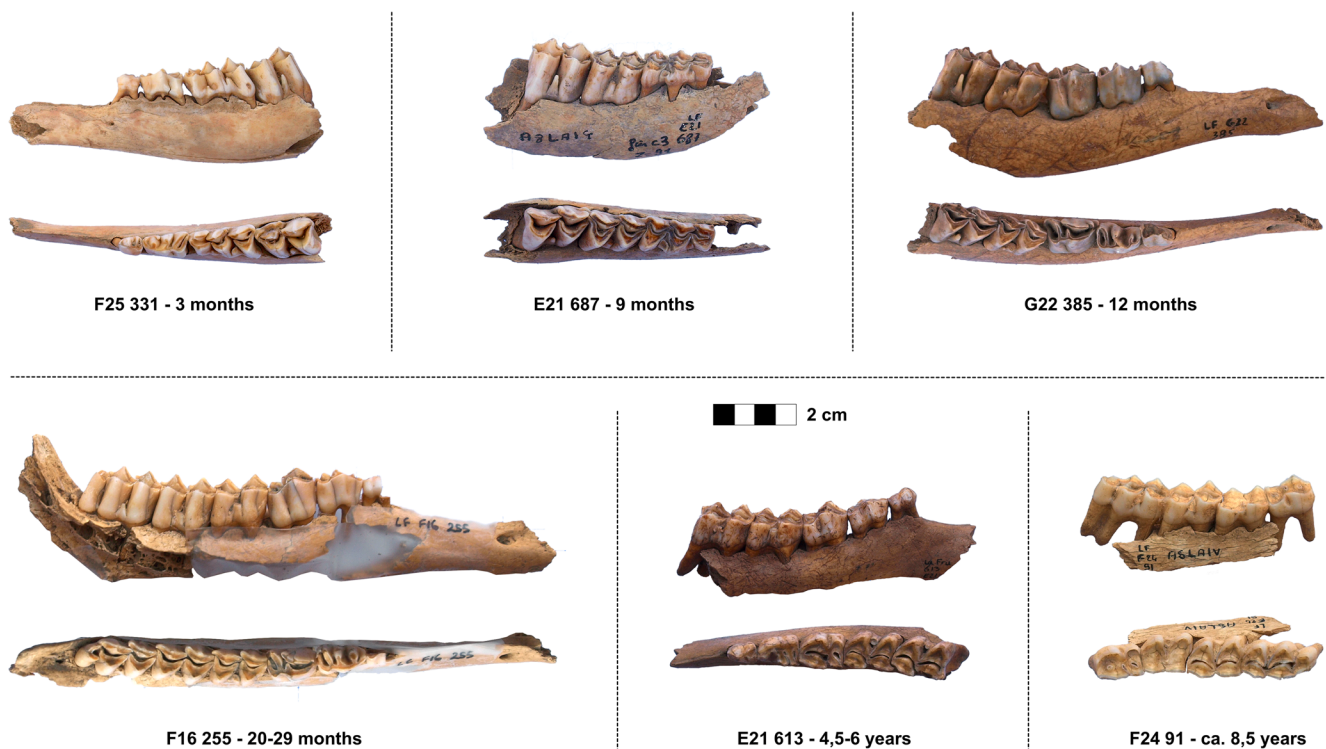
arrows of hunters, although a deliberate avoidance for cultural reasons cannot be ruled out. The fawn then remains with its mother for about 1 year, after which the yearlings are chased out of the parental territory and left to fend on their own. Young, inexperienced and wandering does and bucks may form an easy prey for hunters, as do the oldest adults, often weakened by age. The targeting of such animals may therefore be more an opportunistic procurement than a deliberate hunting strategy, though the latter hypothesis cannot be fully excluded. Further light on this issue is provided by the analysis of the seasonality of roe deer procurement.

### Investigating the seasonality of roe deer procurement

A literature review of the reproductive cycle of the modern roe deer shows that in many European countries, the birth peak occurs between late May and early June (Linnell and Andersen 1998). In our analysis, we defined the first of June as the birth date consensus, taking into consideration the fact that the European populations roughly follow a seasonality gradient, with the latest births occurring in alpine areas and

**Fig. 8** Roe deer skeletal element distribution, expressed as % corrected NISP (NISP of skeletal part divided by anatomical element count). Illustration modified from J.-G. Ferrière, © ArcheoZoo.org





**Fig. 9** Remains of roe deer lower jaws of different age groups from La Fru Layer 3-Area I. Photographs A. Bridault & A. Binois-Roman

southeastern Scandinavia (Linnell and Andersen 1998, p. 501).

The seasons at death were assessed from the 39 individuals estimated to be under 15 months of dental age, which is a relatively large sample for prehistoric contexts. While a few individuals (6/39) were killed between December and April, most seasonality indicators (33 out of 39) fall between May and September (Fig. 11). This is also the period of the highest dispersion for yearlings and older animals, the main targets of the hunt. Indeed, as prime roe bucks begin to establish their territory in March and to shift to solitary behaviour, developed yearlings and young bucks are no longer tolerated in their home range from the end of April to the end of the mating period in August (Geist 1998). Yearling females are also chased out by their mother when the gravid does carve out a nursery territory within that of the adult buck's prior to giving birth in late May. These aterritorial animals (yearlings, sick and old individuals) then wander in poor habitats and undisputed areas on the periphery of clan territories, forming temporary clubs (Geist 1998). The high proportion of subadults killed during the good season is clearly related to the hunting of such aterritorial and dispersed animals. This can also be the case for the older targeted animals. On the contrary, winter is a period of aggregation (of larger groups in open habitats), during which all group members may be encountered feeding together (Sempère

et al. 1996) and group movements are more extensive. No animal among those studied appears to have been killed in October or November, the period during which males shed their antlers and, in some locations, when herds move to lower elevations in advance of the permanent snow cover (Myserud 1999).

Only six antler remains have been identified in the assemblage, providing a single seasonality indicator. They are all beam fragments or tines, with the exception of the skull cap (#F24 298) of an adult roe buck whose complete antlers were retrieved in close proximity; the antlers were detached from the pedicles (onto which they can be refitted), which display a high porosity of the exposed surface (Fig. 12). This indicates that these antlers were about to be shed when the animal died, meaning in the early fall, shortly after the rut, a time when males need to replenish their fat reserves.

The discrepancy between the large number of animals identified by dental age and the paucity of roe deer antlers in the assemblage is striking. The adult males display unshed antlers between January and late September. Yearling buck antlers (spiked or branched) start to grow in February, become fully developed in May, and are shed in October–November. All of the 27 animals killed between 8 and 14 months of age would therefore have sported unshed antlers had they been males. Since antler remains are under-represented in the assemblage, we assume this is related to a hunting strategy,

**Table 4** La Fru Layer 3-Area I: corrected distribution of roe deer lower cheek teeth, according to age class size

	Expected N per individual	NISP	Corrected NISP	% Corrected NISP	MNI	% MNI
Cranium	1	22	22	16.4	3	75
Mandible	2	63	31.5	23.5	4	100
Atlas	1	5	5	3.7	3	75
Axis	1	2	2	1.5	2	50
Cervical	5	0	0	0.0	0	0
Thoracic	13	0	0	0.0	0	0
Lumbar	6	0	0	0.0	0	0
Sacrum	1	0	0	0.0	0	0
Caudal	5	0	0	0.0	0	0
Ribs	26	11	0.42	0.3	1	25
Scapula	2	1	0.5	0.4	1	25
Humerus	2	6	3	2.2	1	25
Radius	2	6	3	2.2	3	75
Ulna	2	8	4	3.0	1	25
Pelvis	2	0	0	0.0	0	0
Femur	2	18	9	6.7	4	100
Tibia	2	6	3	2.2	2	50
Metacarpal	2	19	9.5	7.1	2	50
Vestigial metacarp.	4	5	1.25	0.9	2	50
Metatarsal	2	56	28	20.8	4	100
Phalanx1	8	18	2.25	1.7	2	50
Phalanx2	8	7	0.875	0.7	1	25
Phalanx3	8	4	0.5	0.4	1	25
Vestigial phal.2	8	0	0	0.0	0	0
Vestigial phal.3	8	0	0	0.0	0	0
Talus	2	4	2	1.5	4	100
Calcaneus	2	2	1	0.7	1	15
Naviculocuboid	2	0	0	0.0	0	0
Ex-med cuneiform	2	0	0	0.0	0	0
Malleolar	2	3	1.5	1.1	2	50
Patella	2	0	0	0.0	0	0
Scaphoid	2	2	1	0.7	2	50
Unciform	2	0	0	0	0	0
Lunate	2	2	1	0.7	1	25
Cuneiform	2	1	0.5	0.4	1	25
Capitato-trapezoid	2	3	1.5	1.1	2	50
Pisiform	2	0	0	0	0	0
Total	147		134.298			

mostly targeting sub-adult and adult females. The sex ratio was not investigated through an osteometric analysis, as the material is highly fragmented and sexual dimorphism is known to be weak in the post-cranial skeleton of roe deer (males on average only 1 to 3% larger than females on post-cranial bones, Bosold 1968). It is thus not possible to ascertain

the presence of adult female bones. Nonetheless, the presence of several 3-month-old fawns provides indirect evidence of the hunting of breeding females on maternal territories, which are fairly restricted in size, making them a more predictable prey than males of similar age. Inexperienced subadults and weaker older animals may be easier to capture, especially



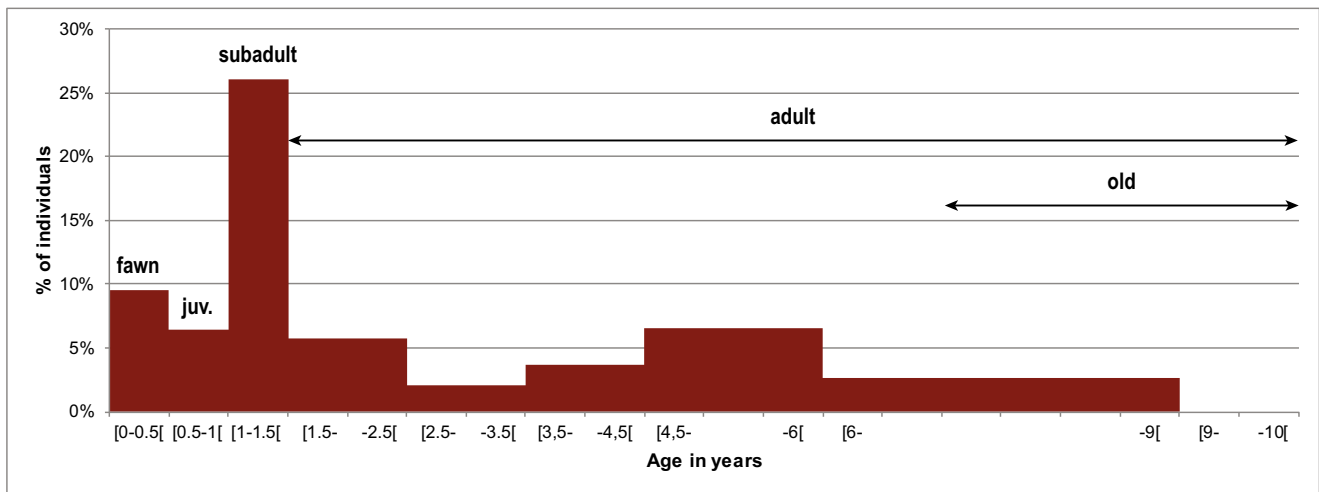


Fig. 10 Mortality profile for roe deer at La Fru Layer 3-Area I (MNI = 94)

when the animals are highly dispersed or roaming across territories.

### Conclusion

The layer 3 at La Fru has yielded one faunal assemblage securely dated to the 15th millennium cal BP, despite stratigraphic issues between Early and Late Azilian layers. Our results bring a clear evidence that the roe deer was already among the high ranked preys and contributed significantly,

with the red deer, to the subsistence of the occupants. The similar number of remains of these two cervids in the faunal assemblage prove that, at La Fru, a reorganization of the subsistence basis occurred at the beginning of the 15th millennium cal BP, as soon as new game resources became available. Stable isotopes provide qualitative evidence of a habitat change that allowed roe deer, an ecologically exigent species, to develop in the area, as is indicated by the animals that were killed at different seasons of the year. Roe deer procurement relied on hunting strategies that targeted sub-adults and older animals, most likely females. This is not a strategy that aims to

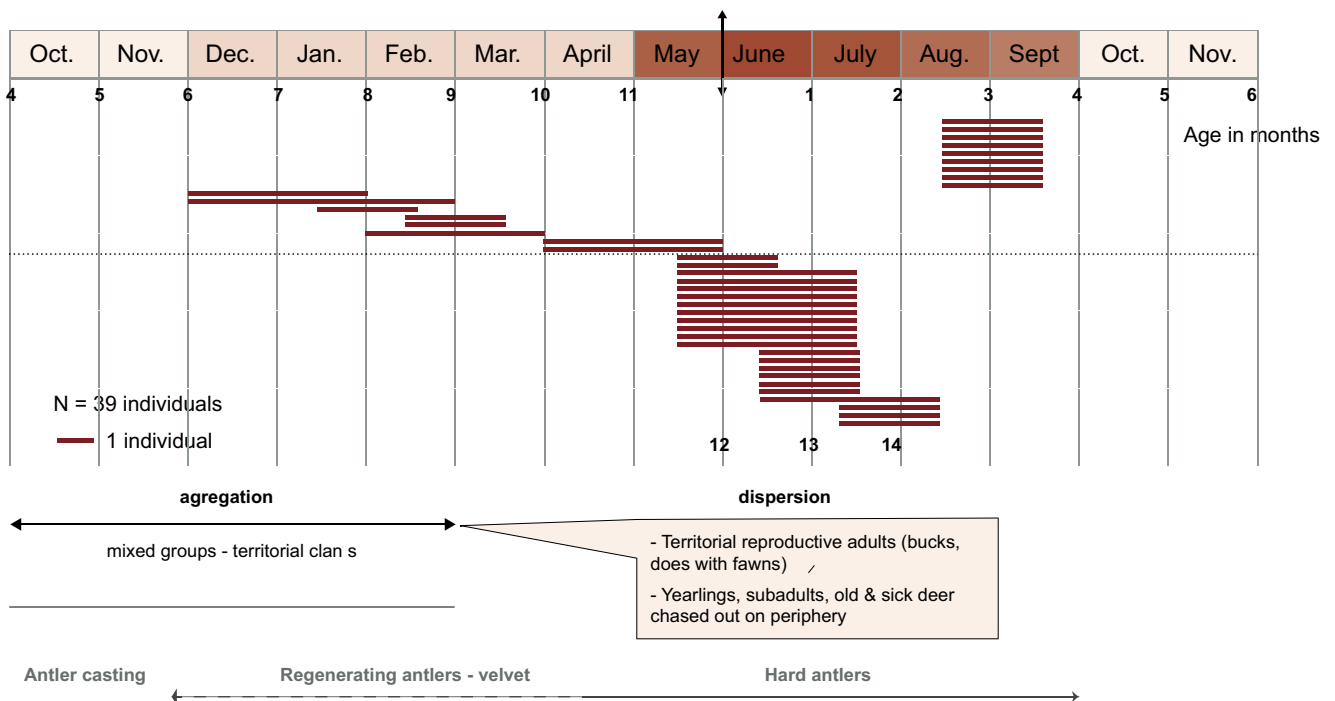


Fig. 11 La Fru Layer 3-Area I: seasons of death of roe deer under 15 months old (MNI = 39)



**Fig. 12** Roe deer skull element found in square F24, Layer 3-Area 1. One of the two antlers has been refitted. Photo G. Pion

maximize returns, as adult males over 3.5 years old are the bulkiest animals<sup>2</sup> but is rather a strategy that requires the least logistical investment (likely individual hunting rather than communal) to ensure a meat and grease supply on a regular basis, at least from early spring to the end of summer. Such an emphasis on roe deer, a game species of lesser interest (in terms of cost-returns) than larger sized prey such as horse, best corresponds to a context of rapid environmental change, to a fauna already reorganized into smaller herds with animals able to hide in the vegetation. Such a strategy could correspond only to the peculiar environmental situation during the Bölling chronozone and not be sustained in the long run. As evidenced at the site of Rochedane in the Jura, the hunters of the late Azilian occupation (dated to 13.3 to 13.5 kyr cal BP) made a quite different choice, relying almost exclusively on red deer prime adult high-risk hunting (Bridault 1994). The episode of significant roe deer hunting at La Fru is thus remarkable by the ecological information it conveys as well as the testimony of a transitional response of human population to major environmental changes.

<sup>2</sup> E.g., in Valais Alps, the average weight of bucks is 19 kg, while that of does is 15 kg (reached by 2.5 years old) (Blant et al. 1998)

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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