

# Integration of Linearbandkeramik cattle husbandry in the forested landscape of the mid-Holocene climate optimum: Seasonal-scale investigations in Bohemia



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## ABSTRACT

Domestic animals and plants were introduced to Europe from the Near East and subsequently spread across Europe, entailing adaptations to different environments with consequences for the biology of organisms, agropastoral technical systems and socio-economic organisation. Agriculture was introduced to Central Europe by Linearbandkeramik (LBK) societies between 5600 and 4900 cal. BC, in predominantly forested environments. LBK farming systems involved intensive permanent field cultivation in natural openings. Milking was practiced as evidenced from cattle mortality profiles and lipid residues in ceramics. Questions arise as to what extent LBK cattle husbandry relied on woodland, and as to whether the seasonal scarcity of fodder conditioned cattle reproduction cycles, with consequences on milk availability. Results from the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  analysis of cattle tooth enamel at Chotěbudice and Černý Vůl (Bohemia, Czech Republic) suggest a limited use of dense forest for cattle herding, even on a seasonal scale: cattle were kept in the open component of the forest/steppe mosaic landscape. Winter forest browsing/provision of leafy fodder was evidenced in one specimen. At Chotěbudice, cattle births mainly occurred over a two to three-month period, suggesting environmental constraints on cattle fertility cycles, and possibly seasonal fodder scarcity. A direct consequence of this would be a shorter period of milk availability throughout the year.

## 1. Introduction

The primary centres of domestication of European cattle, caprines and pigs are located in the Near East and date to the 9th millennium cal BC. These animals were then introduced to Europe at the turn of the 7th millennium with domestic plants and husbandry practices. They spread westward along the Mediterranean margins, on one hand, and following the continental Danubian route, on the other hand, to reach western Iberian coasts during the second half of the 6th millennium and European northwestern coasts at the turn of the 5th millennium. The British Isles were eventually colonized several centuries later (Tresset and Vigne, 2011). During this expansion across Europe, animals and husbandry practices had to adapt to diverse environmental conditions, which differed from those in the Near East (Vigne, 2008). New selection pressures linked to the climate, landscape, dietary resources and pathogens led to the development of new physiological abilities/technical practices regarding reproduction, feeding behaviour, metabolism, animal products and resistance to diseases (Balasse and Tresset, 2007, 2009, 2017; Flori and Gautier, 2013). In this sense, the spread of

domesticates across Europe represents some of the earliest deliberate acclimatisation of domestic animals by human societies. More specifically, environmental factors determine livestock feeding resources and reproductive behaviours, which in turn greatly impact the rhythms of pastoral systems on a seasonal scale. Investigating the extent to which environmental constraints affected agropastoral systems, and the solutions adopted to cope with these constraints, is paramount for a better understanding of how Neolithic economies successfully spread across the diverse climatic zones of Europe.

In Central Europe, agriculture was first introduced by the Linearbandkeramik (LBK) societies. The LBK developed between 5600 and 4900 cal. BC (Price, 2000; Banffy, 2004; Dolukhanov et al., 2005; Pavlů, 2005; Jakucs et al., 2016) over a period of winter warming, summer cooling and increased precipitation (Sanchez Goni et al., 2016). The mid-Holocene climatic optimum led to the retreat of the Pleistocene steppe in Central Europe in favour of the spread of deciduous forests. The degree of openness of these forests has been debated, and a steppe component has also been brought to light in the landscape, the extent of which may have varied considerably in accordance with

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regional macroclimatic differences (Kreuz, 2008; Bogucki et al., 2012; Marinova et al., 2012/2013; Salavert et al., 2014; Pokorný et al., 2015). LBK communities developed farming systems with the following main features. Natural openings were exploited for the intensive permanent field cultivation (Bogaard, 2005; Saqalli et al., 2014) of crops dominated by hulled wheat (einkorn and emmer; Colledge et al., 2005; Jacomet, 2007; Dreslerová and Kočár, 2013). Soil fertility may have been maintained using manure from livestock (Bogaard, 2005; Bogaard et al., 2013). Cattle (*Bos taurus*) were raised as an important component of the animal economy (Bogucki, 1982; Kovačiková et al., 2012; Arbogast and Jeunesse, 2013), even though regional variability has been observed in the relative proportion of cattle among domestic stock, as well as in the role of hunting (Tresset and Vigne, 2001). The analysis of 19 cattle mortality profiles from LBK contexts concluded that milk exploitation was a widespread, although non-intensive, practice across Europe (Gillis et al., 2017). Milk exploitation and transformation were presumed to have been practised in the LBK of Central Europe due to the occurrence of perforated vessels similar to sieves in typology (Bogucki, 1984). Their actual use for cheese making was confirmed by the identification of dairy fat residues in ceramic sieves from the classic to late phases of the LBK (5200–4900 cal. BC) in the region of Kuyavia, Poland (Salque et al., 2012) and at Brodau (LBK classic phase) in Germany (Salque et al., 2013). Dairy fat residues were also retrieved in some instances from non-perforated bowls in the Kuyavia LBK (Salque et al., 2012). Meanwhile, no milk residues were detected in ceramic assemblages from other LBK sites in Saxony and Bavaria in Germany (Salque et al., 2013), or in Bohemia (Mátlová et al., 2017), although the absence of evidence of the use of ceramic vessels for milk collection or processing does not preclude milk exploitation.

These combined elements raise questions concerning the extent to which LBK cattle husbandry developed in the woodland component of the landscape. How was the availability of open grasslands managed throughout the year to feed these large domestic, predominantly grazing herbivores, especially if open lands were cultivated? Palynological evidence indicates pasturing in the floodplains of the river valleys (Kreuz, 2008). The use of forest resources, including woodland grazing and the production of fodder from coppicing and pollarding is often assumed (Kreuz, 2008; Saqalli et al., 2014), building on direct evidence in more recent contexts (lakeside and wetland settlements from the last third of the 5th millennium cal BC onwards; summary in Kühn et al., 2013). It has also been argued that the re-configuration of caprine husbandry by early Neolithic farmers in southeastern Europe, into a cattle pastoral system in the LBK was a consequence of adaptation to a forested landscape, based on the assumption that cattle cope relatively well with forest browsing (Rowley-Conwy and Legge, 2016). However, beyond the environmental perspective, social factors including forms of property have been put forward as the main driving factor for the high representation of cattle in LBK sites (Shennan, 2011; Manning et al., 2013). The use of the forest to feed cattle has actually only been directly tested to a small extent in LBK contexts (see below). The question of subsistence strategies is also paramount, firstly, for a better understanding of how crop cultivation, animal husbandry and forest exploitation were functionally interconnected in LBK economic systems, and secondly, because the management of the cattle diet would have directly influenced animal production. Seasonally-reduced forage availability, especially in wintertime, when meadows are covered with snow and forests do not produce much fodder, could have conditioned cattle reproduction cycles, for which food resources are the main restricting factor (Santos et al., 2006; Burthe et al., 2011). In turn, cattle birth distribution would have partly determined the organization of pastoral tasks throughout the year, but also the availability of milk on a seasonal scale: both elements are key parameters for approaching the socioeconomic modalities of these agropastoral systems.

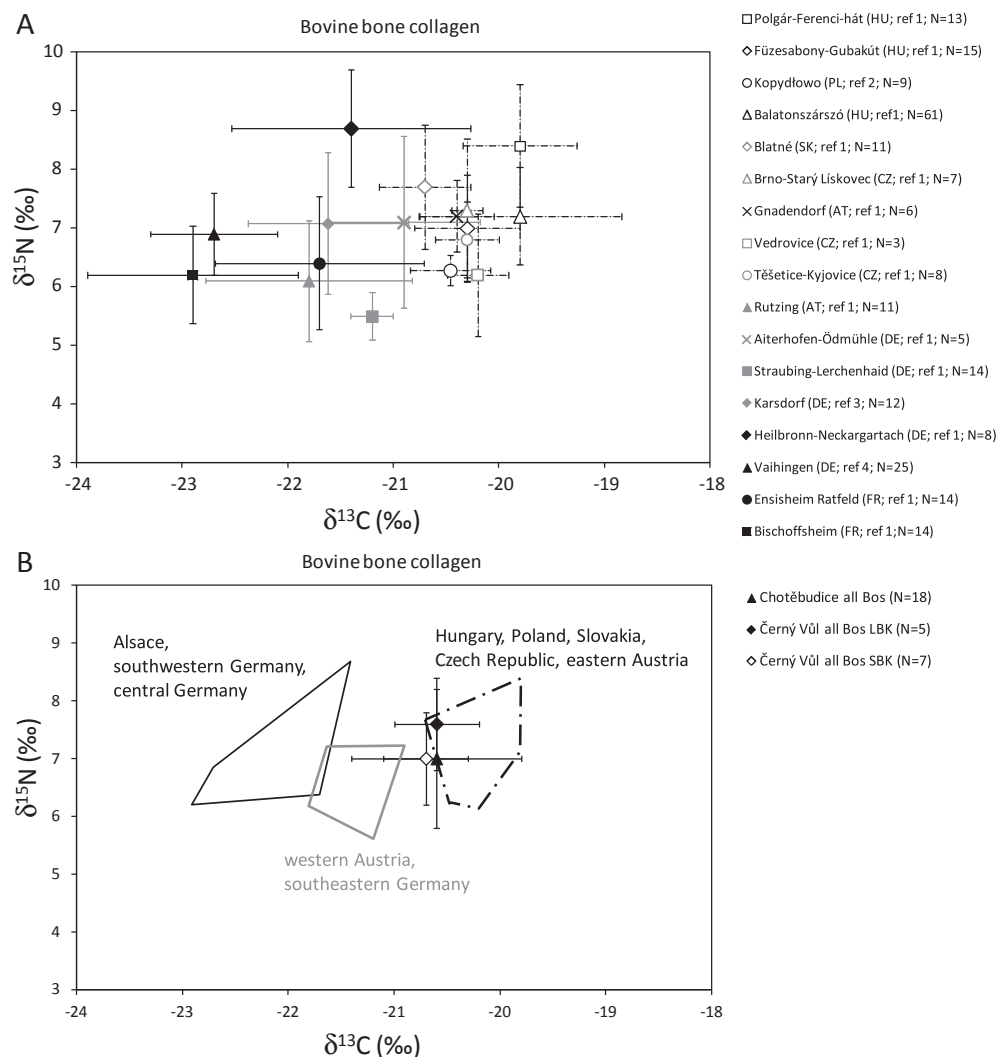
These aspects of LBK cattle husbandry can be investigated using stable isotope analyses of skeletal remains. Previous stable isotope

studies of LBK faunal assemblages consisted in the analysis of bone collagen stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope compositions in order to define the environmental settings. In particular,  $\delta^{13}\text{C}$  values can be used to evaluate the degree of habitat closure: in closed forests, the reduction of light intensity influences photosynthesis efficiency, leading to lower  $\delta^{13}\text{C}$  values in plants (the canopy effect; van der Merwe and Medina, 1991). These values are then passed along the food chain (Drucker et al., 2008). They may therefore be used to test for cattle feeding on forest resources. In this article, we first present a summary of previously published  $\delta^{13}\text{C}$  values in cattle bone collagen in LBK contexts; we show that even though the evidence points to cattle feeding on forest resources in a few sites in the western margin of the LBK extension area, the question remains open in other regions of Central Europe. We then provide two additional  $\delta^{13}\text{C}$  datasets for cattle remains from the LBK sites of Chotěbudice and Černý Vůl in north-western Czech Republic. Feeding on forest resources was additionally investigated on a seasonal scale, through the sequential analysis of stable carbon and oxygen isotope ratios in tooth enamel. Our hypothesis is that stable isotope values measured in bone collagen are less suitable for detecting the seasonal contribution of forest resources to cattle diet than the enamel record. Meanwhile, stable oxygen isotope ratios provide a tool for investigating cattle birth seasonality. Although this parameter has been investigated in other European prehistoric contexts, no data are currently available for the LBK. Studies conducted in the Romanian early Neolithic and Chalcolithic (early 6th and 5th millennium BC; Balasse et al., 2013, 2014), and in the Middle Neolithic in France (early 4th millennium BC; Balasse et al., 2012a), point to restricted birth seasons, compared to year-round breeding in present-day European husbandry where the nutritional status of cattle is maintained to a high level throughout the annual cycle. Although a restricted calving period is also expected for the LBK, this parameter must be directly determined on faunal remains before it can be confidently introduced into models aiming to describing the sustainability of LBK farming systems (for example, Saqalli et al., 2014).

## 2. Previously published $\delta^{13}\text{C}$ datasets from LBK bovine bone collagen

Available datasets of bone collagen stable isotope composition measured on LBK assemblages are summarized in Fig. 1A. Values specifically referred to as “aurochs” in the given publications are not included. However, it must be noted that the “cattle” datasets from the studies in Bickle and Whittle (2013) often potentially include aurochs as a minor component. This is important given that the Holocene aurochs is commonly referred to as a forest animal. The mean  $\delta^{13}\text{C}$  values within each site range from  $-22.9$  to  $-19.8\text{‰}$  but variability within each dataset may be important. In modern ecosystems, the great majority of  $\delta^{13}\text{C}$  values in  $\text{C}_3$  plants (which dominated Neolithic Europe) range from  $-29$  to  $-25\text{‰}$  ( $-26.5\text{‰}$  on average) when growing in open areas (Kohn, 2010). These would lead to  $\delta^{13}\text{C}$  values of  $-27.5$  to  $-23.5\text{‰}$  ( $-25\text{‰}$  on average) in plants from pre-industrial ecosystems (once corrected by  $+1.5\text{‰}$  for the fossil fuel effect: Freyer and Belacy, 1983), and  $\delta^{13}\text{C}$  values ranging from  $-22.5$  to  $18.5\text{‰}$  (mean  $-20\text{‰}$  on average) in collagen (when applying a  $5\text{‰}$  spacing between diet and collagen  $\delta^{13}\text{C}$ ; Ambrose and Norr, 1993). In contrast, late Boreal/early Atlantic aurochs feeding in the dense Atlantic forest in Scandinavia yielded  $\delta^{13}\text{C}$  values ranging from  $-24.2$  to  $-22.4\text{‰}$  (Noe-Nygaard et al., 2005a, 2005b). Considering this, we use the  $-22.5\text{‰}$  value in collagen as a threshold for a major forest component in the diet.

Among the collected datasets for Central Europe, the  $\delta^{13}\text{C}$  values appear to follow a geographical pattern, along a longitudinal gradient (Fig. 1B). The highest  $\delta^{13}\text{C}$  values were measured in the eastern margin of Hungary (settlements of Füzésabony-Gubakút, Polgár-Ferenci-hát and Balatonszárszó; Whittle et al., 2013a), indicating cattle grazing in open areas. The lowest  $\delta^{13}\text{C}$  values were measured in the western margin of southwestern Germany (Vaihingen; Fraser et al., 2013) and in



**Fig. 1.** A – Mean and standard deviation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in LBK bovine bone collagen from Central Europe (AT: Austria; CZ: Czech Republic; DE: Germany; FR: France; HU: Hungary; PL: Poland; SK: Slovakia) (ref 1: Bickle and Whittle, 2013; ref 2: Marciniak et al., 2017; ref 3: Oelze et al., 2011; ref 4: Fraser et al., 2013). Legend from East to West. B – Mean and standard deviation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in bovine bone collagen from Chotěbudice and Černý Vůl, compared to macroregional groups (the convex hulls use the mean values).

eastern France (Bischoffsheim; Bickle et al., 2013a), clearly demonstrating cattle feeding on forest resources. This pattern of variability across Europe is mostly explained by differences in landscape structuration on a macro-regional scale. Indeed, the pollen profiles obtained in southern and western Germany suggest the existence of very thick forests covering most of the territory in these areas (Kalis and Zimmermann, 1988; Kalis et al., 2003). In contrast, a forest-steppe mosaic landscape was reconstructed further east, for example in the Czech Republic, where palynological data, supported by molecular data on the disjunctive floristic and faunistic elements of continental steppes (Kajtoch et al., 2016; Kuneš and Abraham, 2017), the mollusc fauna dwelling exclusively in open habitats (Ložek, 2007; Juříčková et al., 2013; Kuneš and Abraham, 2017), and the presence of chernozem soils (Antoine et al., 2013; Kuneš and Abraham, 2017) all attest to a non-forest component.

Cattle bone collagen from Austria (Gnadendorf and Rutzing; Bickle et al., 2013b), the Czech Republic (Vedrovice, Těšetice-Kyjovice and Brno-Starý Lískovec; Whittle et al., 2013b), Slovakia (Blatné; Whittle et al., 2013b), Poland (Kopydłowo; Marciniak et al., 2017), central Germany (Karsdorf; Oelze et al., 2011) and southeastern Germany (Aiterhofen-Ödmühle, Straubing-Lerchenhaid and Heilbronn-Neckargartach; Dürrwächter et al., 2006; Bentley et al., 2013; Hofmann et al., 2013) showed intermediate mean  $\delta^{13}\text{C}$  values. These datasets also include in some instances a few cattle remains yielding lower  $\delta^{13}\text{C}$  values ( $\leq -23\text{‰}$ ), clearly reflecting forest feeding. The carbon in bone collagen is incorporated from the diet over timescales ranging from

months to years, depending on the species and the individual metabolic state (Libby et al., 1964; Hobson and Clark, 1992). Consequently, bone collagen stable isotope compositions integrate average dietary contributions on a (pluri)annual scale, and intermediate  $\delta^{13}\text{C}$  values could reflect seasonal woodland grazing or leaf foddering. In contrast, tooth enamel retains a chronological record of the stable isotope composition of diet over the duration of tooth formation, which is not consecutively remodelled once enamel mineralization is completed. A seasonal dietary contribution can therefore be demonstrated through the sequential analysis of stable carbon and oxygen isotope ratios in enamel (Balasse et al., 2012a). Here, we tested the hypothesis of the seasonal contribution of forest resources to cattle diet in two additional sites from the Czech Republic.

### 3. Materials and methods

#### 3.1. Description of the archaeological settlements

In the territory of the present-day Czech Republic, the exploitation of animal resources by LBK communities focused predominantly on husbandry. Bovinae (mostly domestic cattle) represent over 40% and up to 85% of the identified specimens (NISP) in these LBK contexts, while small stock (sheep, goats and pigs) play a secondary role in the subsistence economy, with varying respective proportions, possibly due to specific local environmental conditions (Kovačíková et al., 2012). The LBK settlement of Chotěbudice is located in the northwestern part



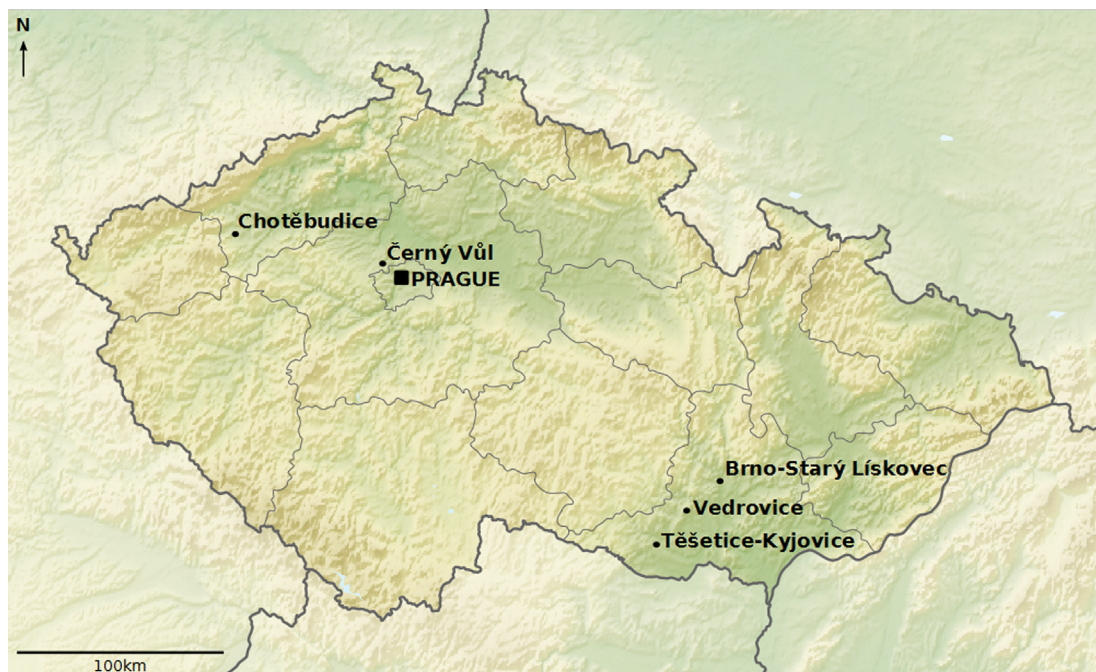


Fig. 2. Map of the Czech Republic with the location of Chotěbudice, Černý Vůl, and Vedrovice, Těšetice-Kyjovice and Brno-Starý Lískovec, the stable isotope data of which are included in the discussion for comparison.

of the Czech Republic (Fig. 2). The site lies at an altitude of 290 m above sea level on a gentle southeast-facing slope close to the Dubá stream. Archaeological excavations revealed nineteen ground plans of long houses and 800 LBK structures spanning a long-term occupation ranging from LBK stages IIa to LBK IIIb, *i.e.*, 5400 to 5100 BCE, as well as a number of features from the Stichbandkeramik (SBK) occupation (Rada, 1981; Šumberová, 1991). Domestic cattle occur as the main species in the archaeozoological assemblage throughout the LBK occupation (Total LBK NISP = 4788. Cattle represent from 63 to 85% of the NISP – depending on the occupation phase, cattle NISP = 314–2017), followed by sheep, goat and pig. Cattle kill-off patterns for the three most representative LBK phases show similar trends over a period of roughly 200 years and suggest a dual exploitation of milk and meat (Kovačiková et al., 2012).

Černý Vůl is located in the Prague-West district (Fig. 2). The site lies at an altitude of 270 m above sea level in the basin of the Únětický stream. Rescue excavations from 1975 to 1977 revealed the ground plans of nine LBK post-hole houses dated to the LBK IIc-IIIb (5200–5000 BCE; Řídký et al., 2008). After a hiatus, the settlement was reoccupied during the latter stage of the SBK IV (4800–4500 BCE; Pavlů and Zápotocká, 2007). Cattle dominate the LBK faunal assemblage, although in lower proportions (43% of NISP; Total LBK NISP = 389) than in Chotěbudice, suggesting variability within the LBK on a regional scale. At this site, the cattle kill-off pattern resembles the pattern established at Chotěbudice, suggesting exploitation for milk and meat (Kovačiková et al., 2012).

### 3.2. Selected bovine remains and attribution to wild or domestic *Bos*

The sample under study included ten cattle lower third molars from the LBK occupation levels at Chotěbudice, five of which (CHO Bos1 to Bos5) had been previously analysed (Kovačiková et al., 2012), and four lower third molars from the LBK occupation levels at Černý Vůl. In addition, thirty bovine (cattle/aurochs) long bones were sampled; 18 of which come from the LBK occupation at Chotěbudice and five from the LBK occupation at Černý Vůl. Seven bovine bones were also selected from the SBK occupation at Černý Vůl. These were used to check for any change in the degree of openness of the landscape over the centuries.

We paid particular attention to the assessment of the domestic status of the selected remains to avoid potential misidentification with its wild counterpart, the aurochs, which is very similar in morphology to the domestic cattle. Aurochs were hunted at Chotěbudice and Černý Vůl although their presence is rare in both assemblages (respectively 1.1 and 0.3% of the LBK faunal assemblages; Kovačiková et al., 2012). The assessment of the domestic/wild status of the selected specimens was based on osteometric criteria for molars and long bones. For the molars, the length and breadth of the neck (following Ducos, 1968) were compared to reference measurements of aurochs' molars (*Bos primigenius*) from Denmark (Degerbøl and Fredskild, 1970) and southeastern France (Helmer and Monchot, 2006). Aurochs from Central Europe are, on average, larger than those from Denmark and southwestern Europe (Bökönyi, 1962; Jarman, 1969; Lasota-Moskalewska and Kobryń, 1990; Guintard, 1999; Wright and Viner-Daniels, 2015). We are aware that size criteria may sometimes be misleading for the distinction between wild and domestic bovines (Vigne et al., 2007; Tresset et al., 2009). However, the selected teeth from Chotěbudice and Černý Vůl are smaller than the rather small aurochs from southeastern France and therefore probably belong to domestic individuals (Supplementary material 1). Only CHO Bos1M3 (from the previous dataset; Kovačiková et al., 2012) measurements overlap with the aurochs dataset. Its status is therefore uncertain.

The attribution of individual long bones to domestic or wild forms is also challenging, partly because the largest domestic individuals mostly overlap in size with small wild females (Degerbøl and Fredskild, 1970; Edwards et al., 2007; Scheu et al., 2008). For this reason, as a precaution, only specimens with measurements falling within the range of variation of the male aurochs from Denmark (Degerbøl and Fredskild, 1970) were attributed to *Bos primigenius*. Specimens smaller than the wild females from Denmark were attributed to *Bos taurus*. All remaining specimens were attributed to *Bos* sp. (Supplementary material 2).

### 3.3. Bone collagen extraction and stable isotope measurements

Collagen was extracted from 320 to 350 mg of bone powder, following the steps described in Bocherens et al. (1991). The analysis was conducted on 400–600 µg of collagen on a Thermo Flash 2000 EA

interfaced with a Thermo DeltaV Advantage IRMS. The analytical precision, determined from 7 to 11 analyses of an alanine standard within each run, was  $\leq 0.06\%$  for  $\delta^{13}\text{C}$  and  $\leq 0.19\%$  for  $\delta^{15}\text{N}$ , and  $\leq 0.5\%$  for C content, and  $\leq 0.3\%$  for N content.

### 3.4. Enamel sequential sampling and stable isotope measurements

Sampling was preferentially performed on the lower M3 hypoconid lobe (for dental nomenclature see [Bärmann and Rössner, 2011](#)) in order to be consistent with previous analyses at Chotěbudice ([Kovačiková et al., 2012](#)), or, failing this, on the protoconid lobe (CerV Bos1M3 and CerV Bos2M3). Both the protoconid and hypoconid lobes were sampled in CHO Bos7M3 and CHO Bos8M3 ([Supplementary material 3](#)), in order to check the consistency of the isotopic sequences between the two lobes of a tooth. Sequential sampling was performed by drilling on the buccal side of the teeth. The number of samples taken from one tooth varies from 15 to 30 for a total number of 359 enamel samples. Enamel samples weighing 5–12 mg were treated in 0.1 M acetic acid (0.1 ml solution/1 mg sample) for 4 h ([Tornerio et al., 2013](#)). Pre-treated enamel samples weighing  $\sim 600\ \mu\text{g}$  were analysed on a Kiel IV device interfaced with a Delta V Advantage IRMS. The accuracy of the data was checked through the analysis of our internal laboratory carbonate standard (Marbre LM normalized to the international standard NBS 19). Over the period of analysis of the samples, the analytical precision within each run, calculated from 6 to 8 measurements of Marbre LM, varies from 0.02‰ to 0.06‰ for  $\delta^{18}\text{O}$  and from 0.01‰ to 0.03‰ for  $\delta^{13}\text{C}$ . Results are expressed in V-PDB.

### 3.5. Interpretation of $\delta^{18}\text{O}$ sequences and modelling

In temperate Europe,  $\delta^{18}\text{O}$  values in skeleton bioapatite from large mammal skeletons are strongly related to  $\delta^{18}\text{O}$  values in local precipitation ([Land et al., 1980](#); [D'Angela and Longinelli, 1990](#)). The  $\delta^{18}\text{O}$  values in precipitation vary seasonally with ambient temperature, with higher values in the summer and lower values in the winter ([Rozanski et al., 1993](#)). This annual cycle pattern is recorded in tooth enamel during mineralization and may be retrieved through sequential  $\delta^{18}\text{O}$  analysis ([Bryant et al., 1996](#), [Fricke and O'Neil, 1996](#)). Because the timing of tooth growth is fixed for a species, inter-individual variability in the positioning of the  $\delta^{18}\text{O}$  cycle within a given tooth is an expression of inter-individual variability in the birth season ([Bryant et al., 1996](#), [Fricke and O'Neil, 1996](#); [Balasse et al., 2003](#)). This variability may be described using the position (distance from the enamel-root junction ERJ), where the highest  $\delta^{18}\text{O}$  value is measured in the tooth crown ([Balasse et al., 2003](#)). This position (thereafter referred to as  $x_0$ ) may be objectively described through the modelling of the  $\delta^{18}\text{O}$  sequence following a cosine-function ([Balasse et al., 2012b](#) and [Supplementary material 4](#)). Modelling also eliminates the effect of variability in tooth size through the normalization of the distance ( $x_0$ ) using the period of the cycle ( $X$ , or the length formed over a year). Inter-individual variability in the period of birth within the annual cycle is then expressed using the ratio  $x_0/X$ , or the distance of the highest tooth crown values, normalized to the period of the cycle which is an expression of the tooth size ([Balasse et al., 2012b](#)).

## 4. Results

### 4.1. Collagen preservation and stable carbon and nitrogen isotope values

The results are reported in [Fig. 3](#) and [Supplementary material 5](#). All the bone samples yielded well-preserved, good-quality collagen. Most collagen extraction yields vary from 20 to 134 mg/g (mean of  $77 \pm 32\ \text{mg/g}$ ). The carbon contents of these extracts vary from 36 to 41% and the nitrogen contents vary from 14 to 16%. Collagen C:N ratios range between 3.0 and 3.2. Two collagen extracts (CHO Bos17 and CHO Bos22) do not fulfil the preservation criteria of a collagen

yield of  $\geq 20\ \text{mg/g}$  (following recommendations by [van Klinken, 1999](#)). However, their %C and %N are within the accepted range (%C > 30 and %N > 11) and their C:N ratios were also consistent with expectations (3.2). Their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are included in the final dataset.

The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values are consistent with the expected range for Neolithic temperate Europe. The  $\delta^{13}\text{C}$  values range between  $-22.9$  and  $-19.5\%$  (mean  $-20.6 \pm 0.7\%$  at CHO and  $-20.6 \pm 0.4\%$  at CerV) and the  $\delta^{15}\text{N}$  values vary between 5.5 and 8.4‰ (mean  $7.0 \pm 1.2\%$  at CHO and  $7.3 \pm 0.8\%$  at CerV) ([Fig. 3](#)). The metacarpal CHO Bos25, identified as an aurochs, stands out with notably low  $\delta^{13}\text{C}$  ( $-22.9\%$ ) and  $\delta^{15}\text{N}$  (3.7‰) values, which will be discussed below. The values measured in the aurochs bones overlap with those measured in *Bos taurus* and *Bos* sp. At Černý Vůl, the bovine specimens from the LBK and SBK occupations yielded similar  $\delta^{13}\text{C}$  values (respectively  $-20.6 \pm 0.4\%$  and  $-20.7 \pm 0.4\%$  on average), suggesting no real change in the degree of openness of the bovines' habitat between the two time periods.

### 4.2. Tooth enamel stable carbon and oxygen isotope values

Results from  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  measurements in enamel bioapatite are reported in [Figs. 4 and 5](#) and [Supplementary material 6](#). In the sequences of  $\delta^{18}\text{O}$  values, the sinusoidal variations in time along the tooth crown, observed on most individuals, reflect the seasonal ambient temperature cycle. The  $\delta^{18}\text{O}$  values vary between  $-9.7$  and  $-2.2\%$ , with an intra-tooth variation amplitude of 2.3 to 5.2‰. Results from the modelling of  $\delta^{18}\text{O}$  sequences are reported in [Supplementary material 4](#). Among the parameters used to describe the  $\delta^{18}\text{O}$  cycles, the  $X$  parameter, *i.e.*, the length of the tooth formed over a year or the cycle period, varies from 29 to 44 mm with a mean value of 36 mm. CHO Bos1M3 stands apart with a significantly longer cycle period (55 mm), in keeping with its larger size ([Supplementary material 1](#)). CerV Bos1M3, CerV Bos2M3 and CerV Bos4M3 could not be modelled due to the absence of two consecutive maximum and minimal values which allow for a secure definition of the length of the cycle. The  $\delta^{13}\text{C}$  values in enamel vary between  $-13.6$  and  $-9.8\%$ . The amplitude of intra-tooth variation is moderate (0.4–1.4‰). CHO Bos9M3 is an exception to this pattern with a higher variation in amplitude (2.4‰), due to lower  $\delta^{13}\text{C}$  values in wintertime ([Fig. 4](#)).

### 4.3. Difference between the protoconid and hypoconid lobes

The  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  sequences measured in the protoconid and hypoconid lobes of CHO Bos7M3 and CHO Bos8M3 are compared in [Fig. 6](#), highlighting a significant shift in both teeth. For each molar, the modelled  $\delta^{18}\text{O}$  sequences are similar in both lobes ( $X = 31.1$  vs 31.8 mm and 43.4 vs 43.9 mm respectively in CHO Bos7M3 and CHO-Bos8M3), reflecting similar enamel deposition and mineralization rates ([Supplementary material 4](#)). However, the position of the optimum  $\delta^{18}\text{O}$  value ( $x_0$ ) shifts by +8.5 mm and +7.9 mm (in CHO Bos7M3 and CHO Bos8M3 respectively) in the hypoconid lobe, compared to the protoconid lobe ([Supplementary material 4](#)). The locations of the highest and lowest  $\delta^{18}\text{O}$  values, as determined from the model, are reported on the tooth crown in [Supplementary material 3](#), where it can be seen that the shift is partly explained by an advanced development of the protoconid compared to the hypoconid lobe. This difference is slightly exacerbated in the highest part of the crown, where the difference in the position of maximum  $\delta^{18}\text{O}$  values is higher than that observed between the minimum values recorded at a later stage of crown growth ([Supplementary material 3](#)). More importantly, most of the shift in the distance can be explained by the lower location of the enamel-root junction (ERJ) in the hypoconid lobe compared to the protoconid lobe, both leading to higher distances for samples in the hypoconid lobe.

As a consequence of this shift, the  $x_0/X$  value calculated in both

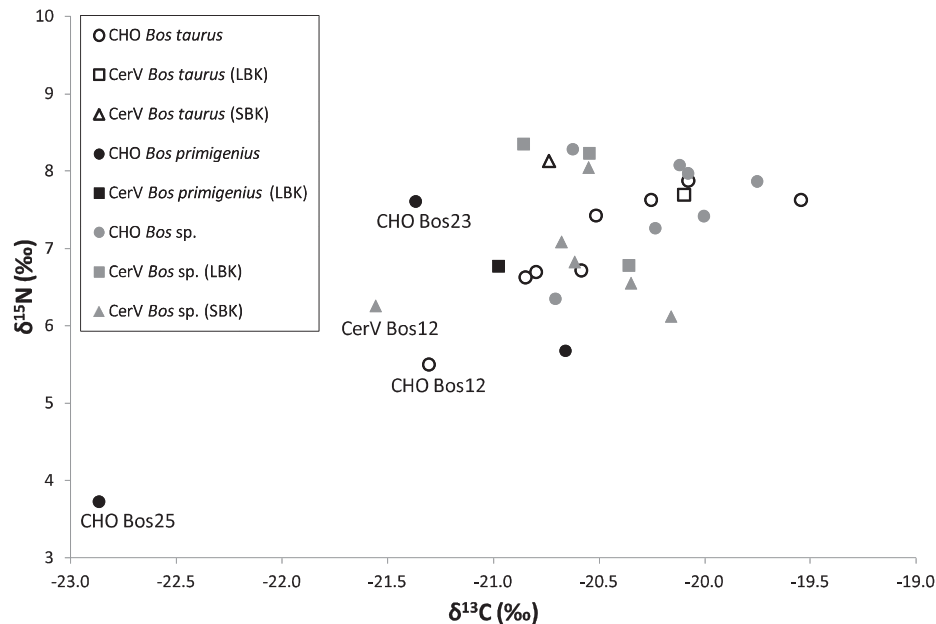


Fig. 3. Results from stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope analysis of bone collagen from Chotěbudice and Černý Vůl *Bos* specimens.

lobes differs by 0.245 (or 24.5% of an annual cycle) in CHO Bos7M3 and 0.17 in CHO Bos8M3 (Supplementary material 4), or approximately three and two months respectively. This precludes a direct comparison of  $x_0/X$  values obtained from the M3 protoconid and hypoconid lobes when investigating birth seasonality. We applied an average correction of  $-0.21$  to the  $x_0/X$  values obtained from hypoconid lobes in order to compare them with previously published protoconid (anterior) lobe values.

#### 4.4. Length of the calving period

Fig. 7 is a representation of inter-individual variability in the tooth crown location of the maximum  $\delta^{18}\text{O}$  value ( $x_0$ , normalised to the length of the tooth formed over a year  $X$  in order to eliminate the effects of tooth size). This variability is an expression of the duration of the annual cycle, over which all individuals were born. At Chotěbudice, most individuals were born over a two to three month period (0.21 or 21% of a yearly cycle). Considering the temporal breadth of the sample (potentially a couple of centuries for the most representative LBK phases at Chotěbudice) and its small size (ten specimens) due to the inherent nature of most archaeological assemblages, caution is required when interpreting the births distribution among what should be considered a palimpsest herd. At Chotěbudice, the cattle kill-off patterns for the different LBK phases show very similar trends over two centuries, suggesting stability in cattle management strategies through time (Kovačiková et al., 2012). Similarly, reduced variability in the calving period may suggest a restricted calving period even over a time scale of centuries. The status of CHO Bos1M3 (domestic vs wild) is uncertain due to the large size of the molar, but it clusters with the main group of individuals, meaning that it was born over the same period of the annual cycle as domestic cattle. The only specimen from Černý Vůl that could be modelled clusters with the main group at Chotěbudice.

## 5. Discussion

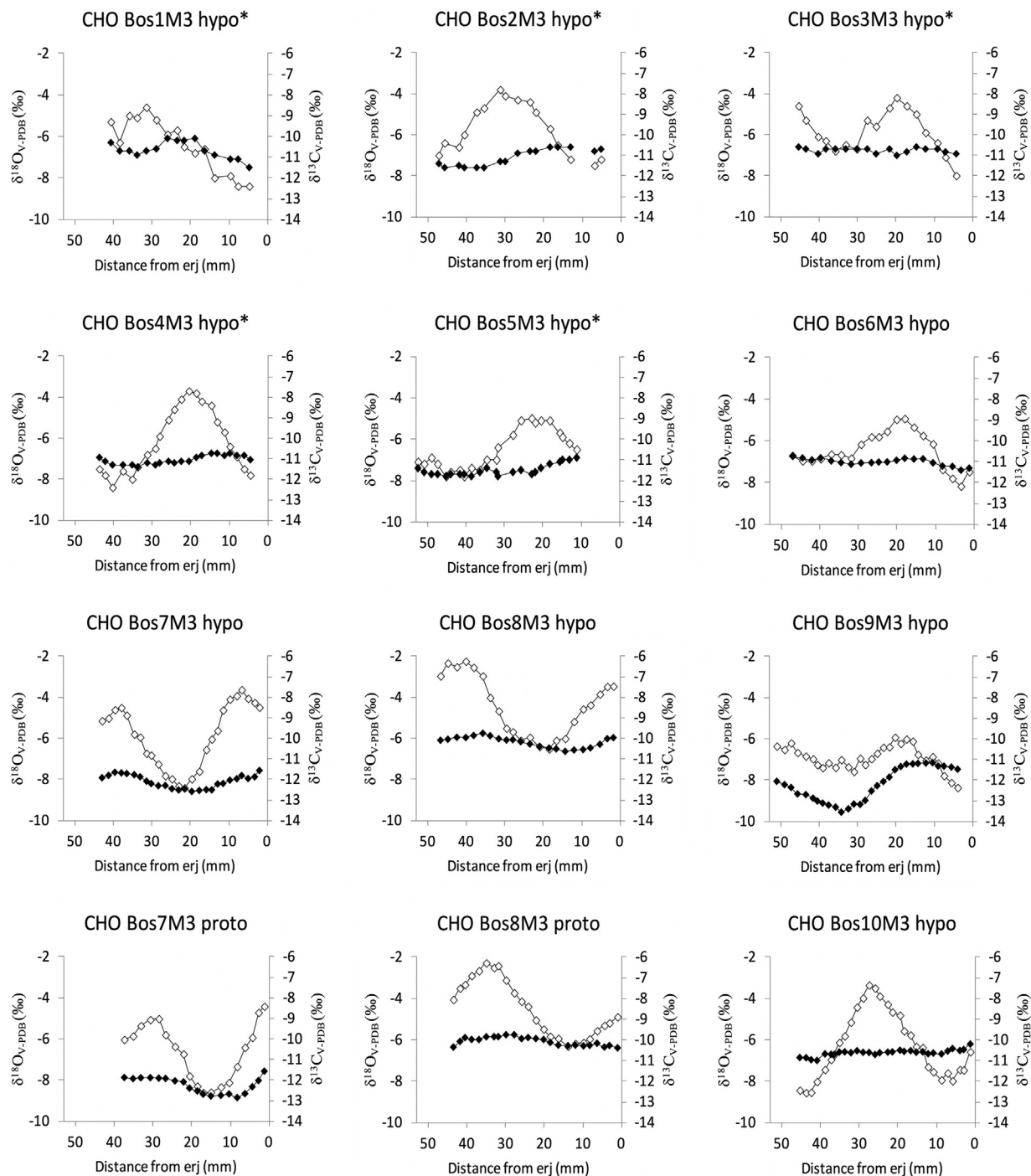
### 5.1. Management of cattle diet

The range of  $\delta^{15}\text{N}$  values and the amplitude of inter-individual variability are similar to those measured in other LBK bovine populations from Central Europe (Fraser et al., 2013; Bickle and Whittle, 2013

and Fig. 1). Further interpretation of this  $\delta^{15}\text{N}$  dataset would require comparisons with values from other animals from local wild and anthropic ecosystems. Most of the  $\delta^{13}\text{C}$  values measured in bovine bone collagen from Chotěbudice and Černý Vůl indicate feeding in open areas ( $> -21\text{‰}$ ). In this regard, they resemble those measured at Vedrovice, Těšetice-Kyjovice and Brno-Starý Lískovec in the south-eastern Czech Republic, averaging  $-20.2\text{‰}$ ,  $-20.2\text{‰}$  and  $-20.3\text{‰}$  respectively (Whittle et al., 2013b and Fig. 1). Analyses of pollen and molluscs from sedimentary sequences in the dry lowlands of northern Bohemia provided evidence for a mosaic landscape with pine-birch forests and a steppe component (Pokorný et al., 2015). At Chotěbudice, anthracological analyses highlighted the presence of oak wood, including an important pine tree component (Kočár et al., 2008) and the existence of a steppe was also suggested from the mollusc fauna (Kovačiková et al., 2012). Indeed, our results could suggest either cattle herding in open-canopy forests or forest boundaries, or preferential grazing on persistent patches of steppe grassland. Nevertheless, a denser forest component in the landscape is also evidenced in the lowest  $\delta^{13}\text{C}$  value of the dataset ( $-22.9\text{‰}$ ), measured in CHO Bos25 (classified among the aurochs based on osteometric criteria). This value is comparable to  $\delta^{13}\text{C}$  values measured in late Boreal/early Atlantic aurochs feeding in the dense Atlantic forest in Scandinavia ( $-24.2$  to  $-22.4\text{‰}$ ; Noe-Nygaard et al., 2005a, 2005b). Three specimens, including one aurochs (CHO Bos23), and one domestic bovine (CHO Bos12) at Chotěbudice, and one *Bos* sp. at Černý Vůl (CerVBos12), yielded intermediary  $\delta^{13}\text{C}$  values ( $< -21\text{‰}$ ), which could also indicate a forest component.

The sequential  $\delta^{13}\text{C}$  values measured in tooth enamel help to clarify the contribution of forest resources to the cattle diet on a seasonal scale. In all individuals but one (CHO Bos9M3), the  $\delta^{13}\text{C}$  values are typical of feeding in open areas all year round. Limited seasonal changes are visible in the  $\delta^{13}\text{C}$  series, although these would be partly attenuated by the enamel mineralization delay (Balasse, 2002). When seasonal trends are observed, the highest  $\delta^{13}\text{C}$  values occur at the end of summer and the lowest at the end of winter, in accordance with the moderate natural variation in the  $\delta^{13}\text{C}$  values of  $\text{C}_3$  plants on a seasonal scale (Smedley et al., 1991). Winter provisioning with dried fodder harvested from meadows, steppe grassland or even cultivated fields has been discussed elsewhere (Saqalli et al., 2014). The harvesting of fodder during the growing season and its postponed use until winter would





**Fig. 4.** Results from stable carbon ( $\delta^{13}\text{C}$ ; black symbols) and oxygen ( $\delta^{18}\text{O}$ ; open symbols) isotope analysis (V-PDB) of cattle tooth enamel bioapatite from Chotěbudice (CHO) (erj = enamel–root junction). \*CHO Bos1M3 to CHO Bos5M3 data from Kovačiková et al. (2012). Sampling on the hypoconid (hypo) or protoconid (proto) lobe.

interfere with the seasonal cycle of variation in plant  $\delta^{13}\text{C}$  values, by increasing winter  $\delta^{13}\text{C}$  values. The moderate inter-seasonal variation in plant  $\delta^{13}\text{C}$  values could in our case restrict the possibility of highlighting this practice, unless the absence of inter-seasonal variations in some  $\delta^{13}\text{C}$  sequences (in CHO Bos10 M3 and CerV Bos2 M3, as opposed to what is observed in CHO Bos2, Bos4, Bos7 and Bos8 for instance; Figs. 4 and 5) might be an indication of this. However, it is not possible to deduce clear evidence of winter foddering with summer grass from this dataset.

In contrast to all the other specimens from Chotěbudice, CHO

Bos9M3 exhibits a higher range of variation in  $\delta^{13}\text{C}$  values ( $-13.6$  to  $-11.2\%$ ), and a marked seasonal variation pattern with lower  $\delta^{13}\text{C}$  values in winter, when  $\delta^{18}\text{O}$  values are lowest. Considering a  $14.1\%$   $^{13}\text{C}$ -enrichment factor between diet and enamel bioapatite (Cerling and Harris, 1999), the lowest  $\delta^{13}\text{C}$  value measured in enamel would correspond to a diet  $\delta^{13}\text{C}$  value of  $-27.3\%$ , reflecting feeding on plants from forest understory (Drucker et al., 2008). Forest exploitation by Chotěbudice LBK settlers (*i.e.* harvesting of logs, dried twigs and shoots) was otherwise evidenced by botanical macro-remains (Kočár et al., 2008). Cattle could have been brought to the forest or fed leaf reserves

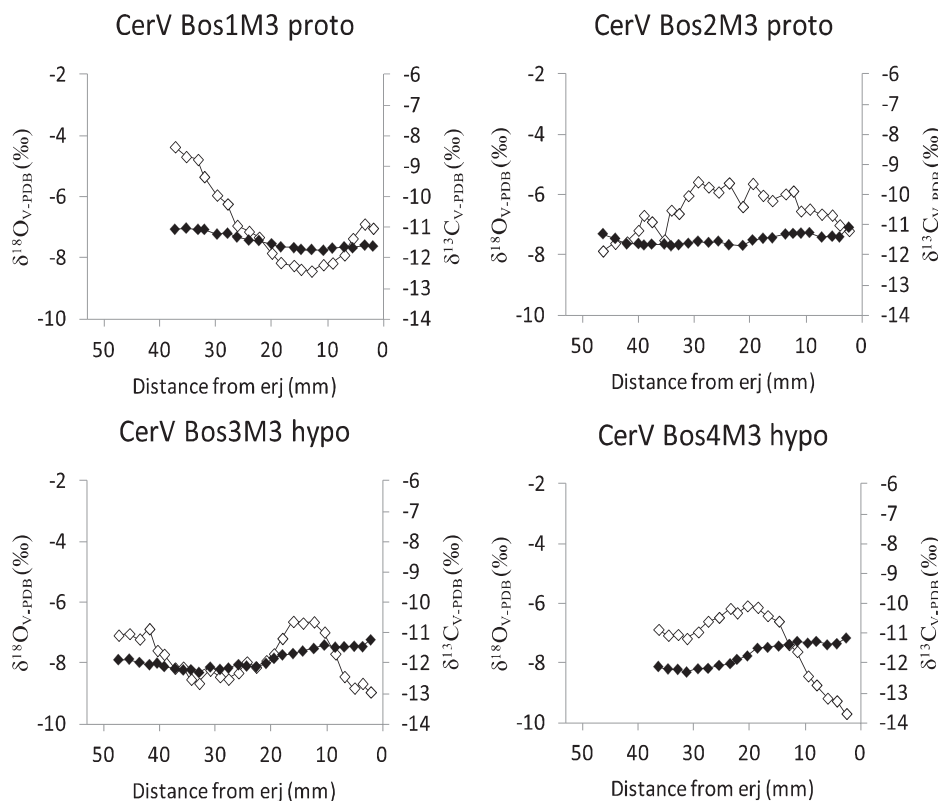


Fig. 5. Results from stable carbon ( $\delta^{13}\text{C}$ ; black symbols) and oxygen ( $\delta^{18}\text{O}$ ; open symbols) isotope analysis (V-PDB) of tooth enamel bioapatite of cattle from Černý Vůl (CerV) (erj = enamel-root junction). Sampling on the hypoconid (hypo) or protoconid (proto) lobe.

collected for this purpose. Winter leaf foddering of cattle has been suggested from similarly low  $\delta^{13}\text{C}$  values in tooth enamel at Măgura-Boldul lui Mos Ivănuș (Starčevo-Criș I phase, early 6th millennium cal BC) in Romania (Balasse et al., 2013). At Măgura, this low winter  $\delta^{13}\text{C}$  signature was only observed in one individual (among five), suggesting a similar system to that described at Chotěbudice. At both sites, winter leaf foddering did not seem to be a prevailing practice but could rather have been a response to an unusually difficult winter, unlike what was shown for instance at the Middle Neolithic site of Bercy (4th millennium BC) in northern France, where this pattern occurred more systematically (Balasse et al., 2012a). Nevertheless, although the low  $\delta^{13}\text{C}$  values measured in CHO Bos9M3 actually indicate a dense forest component in the surrounding landscape, the absence of such signals in all other cattle teeth does not totally preclude the gathering of tree

branches from forest margins, in areas where the canopy effect on plant  $\delta^{13}\text{C}$  values would not apply.

Seasonal feeding on forest resources would not imprint bone collagen as heavily as a year-round contribution. We tried to evaluate how such seasonal contributions would be reflected in bone collagen values on a pluri-annual scale, using the sequences measured in CHO Bos9M3 with winter feeding on forest resources. In order to compare enamel sequential  $\delta^{13}\text{C}$  values and bone collagen  $\delta^{13}\text{C}$  values: (1) a mean annual value was calculated from the sequential  $\delta^{13}\text{C}$  values measured in enamel over an annual cycle (using the period X), starting from the apex; (2) the latter value was transposed to diet using a 14.1‰  $^{13}\text{C}$ -enrichment factor between diet and enamel bioapatite (Cerling and Harris, 1999); (3) diet values were transposed to collagen applying 5‰ spacing between diet and collagen  $\delta^{13}\text{C}$  (Ambrose and Norr, 1993). The

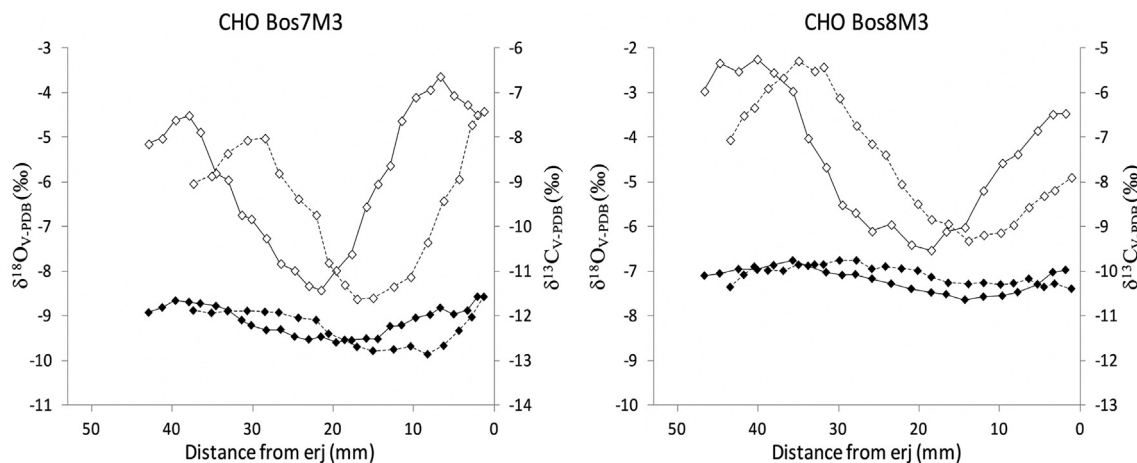
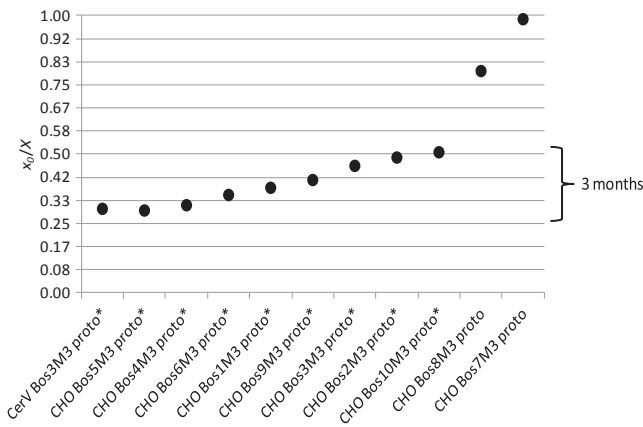


Fig. 6. Results from stable carbon ( $\delta^{13}\text{C}$ ; black symbols) and oxygen ( $\delta^{18}\text{O}$ ; open symbols) isotope analysis (V-PDB) of tooth enamel bioapatite of cattle from Chotěbudice. Comparison between the hypoconid lobe (continuous line) and the protoconid lobe (dashed line). In CHO Bos7M3, the higher  $\delta^{18}\text{O}$  values in the hypoconid lobe are due to the accidental use of a more concentrated acetic acid during the pre-treatment (Supplementary material 3).





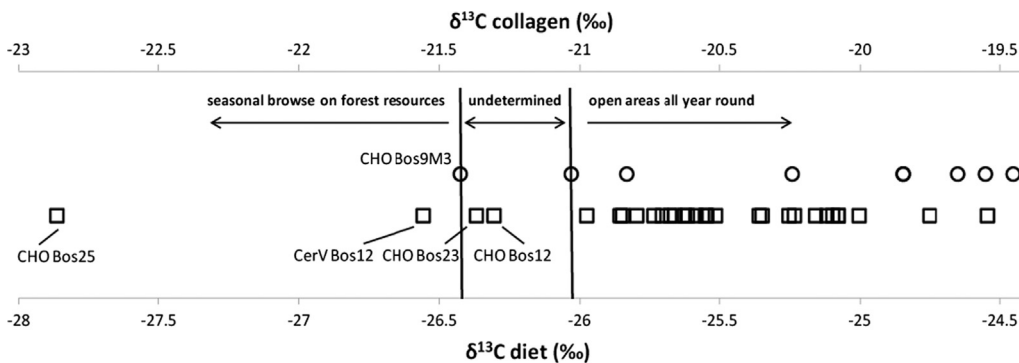
**Fig. 7.** Cattle birth distribution, expressed by inter-individual variability in the position of the maximum  $\delta^{18}O$  values ( $x_p$ ) normalized by the period ( $X$ ) of the  $\delta^{18}O$  in the lower M3 from Chotěbudice (CHO) and Černý Vůl (CerV). Values obtained on the protoconid lobe. \*Values calculated from those obtained on the hypoconid lobe with a correction of  $-0.21$ .

enamel sequential  $\delta^{13}C$  values measured in CHO Bos9M3 would correspond to a bone collagen  $\delta^{13}C$  value of  $-21.4\%$ . This value falls within the intermediate  $\delta^{13}C$  values measured in LBK settlements in Europe as a whole (Fig. 1), which would not necessarily demonstrate cattle feeding on forest resources. It is therefore possible that this practice could have been overlooked in bone collagen datasets.

Fig. 8 compares the estimated diet  $\delta^{13}C$  value of CHO Bos9 M3 (as a reference for seasonal feeding on dense forest resources) and other cattle M3s (as references for grazing in open areas all year round) to the bone collagen values obtained from bovine bone collagen at Chotěbudice and Černý Vůl. The undetermined zone, between the lowest value estimated for feeding in open areas ( $\delta^{13}C$  collagen  $-21.03\%$ ) and the value estimated for CHO Bos9M3 is very narrow, highlighting once again the lack of resolution of the bone collagen dataset to investigate diet on a seasonal scale. One *Bos primigenius* (CHO Bos23) and one *Bos taurus* (CHO Bos12) fall within this undetermined zone. Apart from the aurochs CHO Bos25, with an outstandingly low bone collagen  $\delta^{13}C$  value ( $-22.9\%$ ), one *Bos* sp. from Černý Vůl (CerV Bos12, from the SBK occupation) falls within the range of values possibly reflecting seasonal feeding on forest resources. These occurrences are in a minority compared to all the remaining samples with bone collagen  $\delta^{13}C$  values higher than  $-21\%$ , reflecting feeding in open areas all year round. In conclusion, our data from Chotěbudice and Černý Vůl suggest either a limited occurrence of dense forests in the area, or a limited use of forests for cattle herding by LBK farmers.

### 5.2. Cattle birth seasonality

Domestic cattle are physiologically capable of breeding throughout the year, with no interruption in fertility. However, food resources are a



**Fig. 8.** Stable carbon isotope ratios ( $\delta^{13}C$ ) of the diet of cattle from Chotěbudice and Černý Vůl, estimated from values measured in tooth enamel (circles) and in bone collagen (squares).

major restricting factor in reproductive performances and in the survival probability of offspring (Burthe et al., 2011). The present-day pattern of year-round calving is only observed in herds provided with shelter and artificial food all year long. In contrast, cattle populations living in unmanaged conditions exhibit seasonal reproduction in synchrony with vegetation dynamics (Lecomte and Le Neveu, 1986). Aseasonal breeding has been observed in Chillingham cattle feral populations, in north-eastern England (Hall and Hall, 1988) but this characteristic is predicted to reflect selection as a result of their previous history of domestication (Burthe et al., 2011). At Chotěbudice, the restricted birth period (two to three months) observed in bovines resembles that described for modern free ranging cattle of the hardy Highland cattle breed living in northern France, with calving occurring mostly between May and July (Lecomte and Le Neveu, 1986), and in Germany with calving occurring in March and April (Reinhardt et al., 1986). The Grey cattle bred today in the Thrace region of Turkey, extensively raised with no feeding supplements, or only a little in very cold winters, also give birth over a two-month period in March and April (Soysal and Kök, 2008). This strongly suggests environmental constraints on the reproductive cycle of livestock at Chotěbudice. In spite of moderate climate seasonality, and mild and wet winters during the time period considered here (Kalis et al., 2003; Sánchez Goñi et al., 2016), seasonal scarcity in grazing resources may have been a limiting factor for the female fertility rate. Indeed, our stable isotope dataset suggests that food supplements in winter were far from systematic in the studied assemblage. Nevertheless, this constraint was not major, as evidenced by the presence of two outliers (CHO Bos7M3 and CHO Bos8M3), demonstrating the survival of calves born out of the main calving season to adulthood (Fig. 7). Out of season births are reported in free ranging cattle herds with seasonal calving: in the semi-wild Scottish Highland breed, cattle kept with minimal management in the Rhein-Taunus Naturpark in Germany, only 9% of the births were reported to occur out of the main calving season (Reinhardt et al., 1986). Interestingly, the presence of these outliers might also reflect the absence of strong control on cattle reproduction by LBK herders.

Similar datasets from the LBK are not available for comparison. Cattle birth seasonality at the earlier Neolithic site of Măgura-Boldul lui Mos Ivănuș (early 6th mill BC) was investigated on a limited number of specimens (four) and on the upper third molar, precluding direct comparison (Balasse et al., 2013). At Cheia in Romania, where the Hamangia occupation (5200–4950 cal BC) spanned the latter part of the occupation at Chotěbudice (LBK IIC to LBK IIIB), cattle birth distribution occurred over a similar timescale (3 months) to the LBK site and over the same period of the year, although maybe with a slightly earlier start (Balasse et al., 2014). At the Middle Neolithic site of Bercy in Paris, France (beginning of the 4th mill BC), cattle births extended over two additional months. This pattern could have been favoured by a recurrent winter contribution of forest resources to the cattle diet (Balasse et al., 2012a).

At Chotěbudice, a restricted calving period would have directly impacted the period of milk availability throughout the year. Firstly,

this is because shorter lactation may be assumed for Neolithic hardy cows compared to present-day cattle: figures of 6 to 8 months are reported in the literature for modern European unimproved cattle breeds (Peške, 1994; Tresset, 1996; Bignal et al., 1999). Secondly, it is rather unlikely that each cow gave birth to a calf every year: in cattle the 280 day gestation period is followed by an interval between calving and the next conception, which may greatly vary according to the nutritional state (Ball and Peters, 2004). For example a median figure of 174 days is given for the Chillingham unmanaged herd of white cattle in northern England, meaning a calving interval of 454 days (Hall and Hall, 1988). In the free-ranging Highland cattle of the Marais Vernier, showing a strongly seasonal breeding pattern, food scarcity may also lead to females simply skipping the mating period until the following year (Lecomte and Le Neveu, 1986). In such conditions, maintaining a level of milk production throughout the year would have been possible in the case of aseasonal breeding, but would have been more critical if breeding was restricted to a two to three-month period. The reduced availability of fresh milk could have been overcome by storing dairy products in the form of cheese. As mentioned above, ceramic sieves dated to the classic and late phases of the LBK have been identified in Poland and Germany, demonstrating that these communities mastered the technology for cheese making (Bogucki, 1984; Salque et al., 2012, 2013). However, no such evidence was found in Bohemia, where no perforated potsherd has yet been reported for the LBK, and where a recent study on a ceramic assemblage from the late LBK phase at Bylany (N = 163) did not reveal any milk lipid residues (Mátlová et al., 2017). Even though the absence of milk residues in ceramic potsherds does not preclude milk processing in perishable containers, for now there is no archaeological evidence for cheese making in the area under study. Consequently, the use of storable dairy products by LBK farmers in Bohemia is still uncertain.

## 6. Conclusions

Previous stable isotope analyses in LBK bovine remains from the western area of the LBK (southern and western Germany, eastern France) have shown the reliance of cattle husbandry on resources from the thick forests occupying most of the territory in these zones. In contrast, bone collagen  $\delta^{13}\text{C}$  data from other parts of central Europe (Hungary, western Slovakia, the Czech Republic, Poland and Austria) suggest that cattle herding predominantly took place in open areas, although with low resolution on a seasonal scale. The sequential analysis of  $\delta^{13}\text{C}$  values in enamel conducted in the present study introduced the seasonal dimension of diet management/landscape exploitation by LBK herders, with important outcomes. The majority of cattle from Chotěbudice and Černý Vůl grazed in open areas all year round. This suggests that cattle were mainly kept in the steppe component of the forest/steppe mosaic landscape prevailing at this time in Bohemia. These results do not preclude the gathering of tree branches from forest margins, in areas where the canopy effect on plant  $\delta^{13}\text{C}$  values would not apply: the  $\delta^{13}\text{C}$  signal may reach its limit in this regard. Meanwhile, the presence of a dense forest component was confirmed in the low  $\delta^{13}\text{C}$  value measured in one aurochs bone, and the seasonal exploitation of this dense forest was also evidenced in one domestic bovine as winter browsing/provision of fodder. The estimation of a bone collagen value based on the integration of this seasonal signal on a (pluri)annual basis also led to the conclusion that such a contribution may have been largely overlooked when bone collagen  $\delta^{13}\text{C}$  values alone were taken into consideration. Future research should adopt this analytical strategy as a complement to bone collagen analysis, in order to refine our understanding of the modalities of forest exploitation by LBK herders on a seasonal scale, which is the required scale for the analysis of agropastoral systems.

The definition of the key parameter of cattle birth distribution is also essential in order to obtain a clearer picture of work organisation and animal product availability. This study provides the first dataset on

LBK cattle birth seasonality. At Chotěbudice, cattle births were shown to occur mainly over a restricted two to three-month period, suggesting environmental constraints on the cattle fertility cycle, and possible seasonal fodder scarcity in a context where our stable isotope dataset did not evidence recurrent food supplements in wintertime. A direct consequence of a short birth period would be a relatively short period of milk availability. In the absence of archaeological evidence for cheese making in the LBK of Bohemia, uncertainty persists as to whether dairy resources may have been secured by transforming them into storable products. The development of similar works on other LBK assemblages will help to define whether the traits identified at Chotěbudice are typical of LBK husbandries, or whether regional diversity can be brought to light. We thus call for the multiplication of such studies in order to provide models with direct evidence of husbandry practices and zoo-technical parameters.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jaa.2018.05.002>.

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