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PO Box 117  
221 00 Lund  
+46 46-222 00 00



# Interdisciplinary analyses of the remains from three gallery graves at Kinnekulle: tracing Late Neolithic and Early Bronze Age societies in inland Southwestern Sweden

Malou Blank<sup>1</sup> · Anna Tornberg<sup>2</sup> · Karl-Göran Sjögren<sup>1</sup> · Corina Knipper<sup>3</sup> · Karin M Frei<sup>4</sup> · Helena Malmström<sup>5</sup> · Magdalena Fraser<sup>5</sup> · Jan Storå<sup>6</sup>

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## Abstract

In this paper, we investigate the Scandinavian Late Neolithic and Early Bronze Age of Kinnekulle in southwestern Sweden. The above-mentioned periods in the study area are poorly understood and the archaeological record consists of a few stray finds and a concentration of 20 gallery graves. This study focuses on three of the gallery graves where commingled skeletons from successive burials were recovered. The human remains and the artefacts from the graves were used for discussing individual life stories as well as living societies with the aim of gaining new knowledge of the last part of the Neolithic and the beginning of the Early Bronze Age in southwestern Sweden. We focused on questions concerning health and trauma, mobility and exchange networks, and diet and subsistence of the people using the graves. Chronological, bioarchaeological, and biomolecular aspects of the burials were approached through the application of archaeological and osteological studies, as well as stable isotope, strontium isotope, radiocarbon, and mtDNA analyses. The study provides evidence for high mobility and diverse diets, as well as inhumations primarily dated to the transition between the Late Neolithic and Early Bronze Age. We suggest that the mountain plateau of Kinnekulle was mainly reserved for the dead, while the people lived in agriculture-based groups in the surrounding lower lying regions.

**Keywords** Scandinavian Late Neolithic and Early Bronze Age · Gallery graves · Isotope analyses · Health · Trauma · Subsistence · Mobility

## Introduction

The Scandinavian Late Neolithic (LN: ca. 2200–1700 BC) and Early Bronze Age (EBA: ca. 1700–1100 BC) are often described as a time of major socioeconomic transformations, characterized by increased social complexity, growing population density, complex bifacial flint-working techniques, the continued development of long-house construction, the construction and use of gallery graves, intensified import of gold and copper artefacts, and a stronger reliance on agriculture compared to the Middle Neolithic (MN: ca. 3300–2200 BC, Apel 2001; Artursson 2009; Kristiansen and Larsson 2005; Simonsen 2017; Vandkilde 1996). In the Nordic context, most research has concentrated on the Danish isles and Scania in southern Sweden (e.g. Artursson 2009; Bergerbrant et al. 2017; Ebbesen 2007; Frei et al. 2019; Frei et al. 2015; Kristiansen and Larsson 2005; Simonsen 2017; Skoglund 2005; Tornberg 2018; Vandkilde 1996), although eastern and central Sweden have also been

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✉ Malou Blank  
malou.blank.backlund@gu.se

<sup>1</sup> Department of Historical Studies, University of Gothenburg, Gothenburg, Sweden

<sup>2</sup> Department of Archaeology and Ancient History, Lund University, Lund, Sweden

<sup>3</sup> Curt-Engelhorn Center for Archaeometry, Mannheim, Germany

<sup>4</sup> National Museum of Denmark, Environmental Archaeology and Materials Science, Kongens Lyngby, Denmark

<sup>5</sup> Human Evolution, Department of Organismal Biology, Uppsala University, Uppsala, Sweden

<sup>6</sup> Osteoarchaeological Research Laboratory, Department of Archaeology and Classical Studies, Stockholm University, Stockholm, Sweden

studied (Apel 2001; Eriksson et al. 2008; Fraser 2018). The LN and EBA in inland southwestern Sweden are less intensively studied (Weiler 1994) and rarely included in the discussions of the suggested social changes. Nevertheless, in recent investigations (Blank 2019, 2021; Blank et al. 2018a, 2020, 2021), new data from the megalithic population of Falbygden, inland southwestern Sweden demonstrate that major changes occurred during the LN and EBA involving a distinct increase in human mobility and genetic diversity, as well as more varied agro-pastoral subsistence practices in comparison to the MN period. By further investigating this inland region, being outside the core geographical area of LN-EBA research, our study provides a widened understanding of LN-EBA societies.

In the archaeological record from the LN and EBA, the inland of southwestern Sweden stands out from the general picture of south Scandinavia. Some of the differences, such as the few LN flat graves and long houses, may be a consequence of the low number of large-scale excavations in the area. However, the large LN gallery graves as well as the relatively low profiled Bronze Age cairns in this area compared to the small gallery graves and large BA mounds in Denmark and Scania can be assigned to regional variation (Blank 2021; Weiler 1994).

In inland southwestern Sweden, archaeological remains from settlements are poorly known and most of the excavated graves from the LN and EBA are collective graves with successive burials containing commingled and fragmented skeletons (Blank 2021; Weiler 1994). In these cases, the conventional archaeological methods are limited and the conditions for osteological studies are challenging. However, by including bioarcheological methods, we can gain new knowledge about the individuals buried in these graves and make assumptions about the LN and EBA populations and social development in the area.

This study focuses on Kinnekulle, immediately south of lake Vänern in the region of Västergötland (VG, Fig. 1). Kinnekulle is a plateau mountain with sedimentary layers covered by diabase and surrounded by much older bedrock. The limestone rich area provides good conditions for bone preservation and the geological differences between Kinnekulle and the surrounding regions make it an ideal setting for mobility studies based on strontium (Sr) isotopes.

The aim of this study is to investigate human mobility and dietary patterns of LN and EBA individuals buried at Kinnekulle. The investigation is based on interdisciplinary analyses of the remains from 18 humans and analyses of artefacts recovered in three gallery graves (Supplementary Information, SI 1 and 2). The graves represent typical southwestern Swedish gallery graves, characterized by port-holes, ante-chambers, and rather large sizes of about 5 to 14 m.

We investigate health and dietary patterns and discuss subsistence strategies by combining osteological

investigations, bioarcheological data, and nitrogen and carbon isotope analysis. The Sr isotope data and the artefacts within the graves provide information on possible settlement patterns, landuse, and human movements. The radiocarbon dates in combination with the artefacts enable us to estimate the use time of the graves. Furthermore, we compare our results to data from previously analysed megalithic populations from Falbygden (Blank 2021).

## Kinnekulle

### Geology and Sr isotope baseline data

Most of southwestern Sweden consists of Precambrian crystalline rocks from the Early and Middle Proterozoic eras (Andersson et al. 1999; Larsson and Tullborg 2015). The 7×13 km large Kinnekulle on the other hand is one of three areas within inland southwestern Sweden characterized by Palaeozoic sedimentary rocks (Fig. 1). These rocks once covered large areas, of which now only some areas remain due to diabase caps protecting them from the glacial ice. The sediments include Cambrian, Ordovician, and Silurian alum shale, limestone, and slate, on top of sandstone deposited during the lower Cambrian (Larsson and Tullborg 2015).

A recent baseline study (Blank et al. 2018b) confirmed that the isotopic composition of the bioavailable Sr more or less mirrors the basement geology of the area, with higher ratios in the Precambrian terrains and lower ratios in the Palaeozoic sedimentary areas. According to this study, the local  $^{87}\text{Sr}/^{86}\text{Sr}$  range of Kinnekulle was estimated to be 0.714 to 0.719, including 100% of the observations. This range is based on eight reference samples of spring and creek water from different locations on various lithologies within Kinnekulle (Blank et al. 2018b). The baseline of Kinnekulle is distinctly different from the Sr isotope ranges in the surrounding areas, although there are some overlaps with other sedimentary regions (see “Method”).

### The archaeological record

The archaeology of the area is poorly known and is mainly based on stray finds and a few graves. The stray finds dating to the LN and earlier are concentrated to the periphery and surroundings of Kinnekulle, while the sedimentary area seems rather empty of these artefacts (Blomqvist/Bägerfeldt 1990). Furthermore, Kinnekulle is relatively empty also of EBA stray finds compared with the surrounding areas (Weiler 1994: 45, 96). In the southeastern margin of Kinnekulle, the largest rock carving site in inland southwestern Sweden (Flyhov) is found, with several panels and about 400 figures (Ekhoﬀ 1892; Fig. 2). The rock art displays many similarities to carvings recovered at the west coast, with for

**Fig. 1** Overview of southern Sweden with the distribution of megalithic graves in the south-western part. **A:** lake Vänern, **B:** lake Vättern, 1: Kinnekulle, 2: Falbygden, and 3: Halle and Hunne mountains



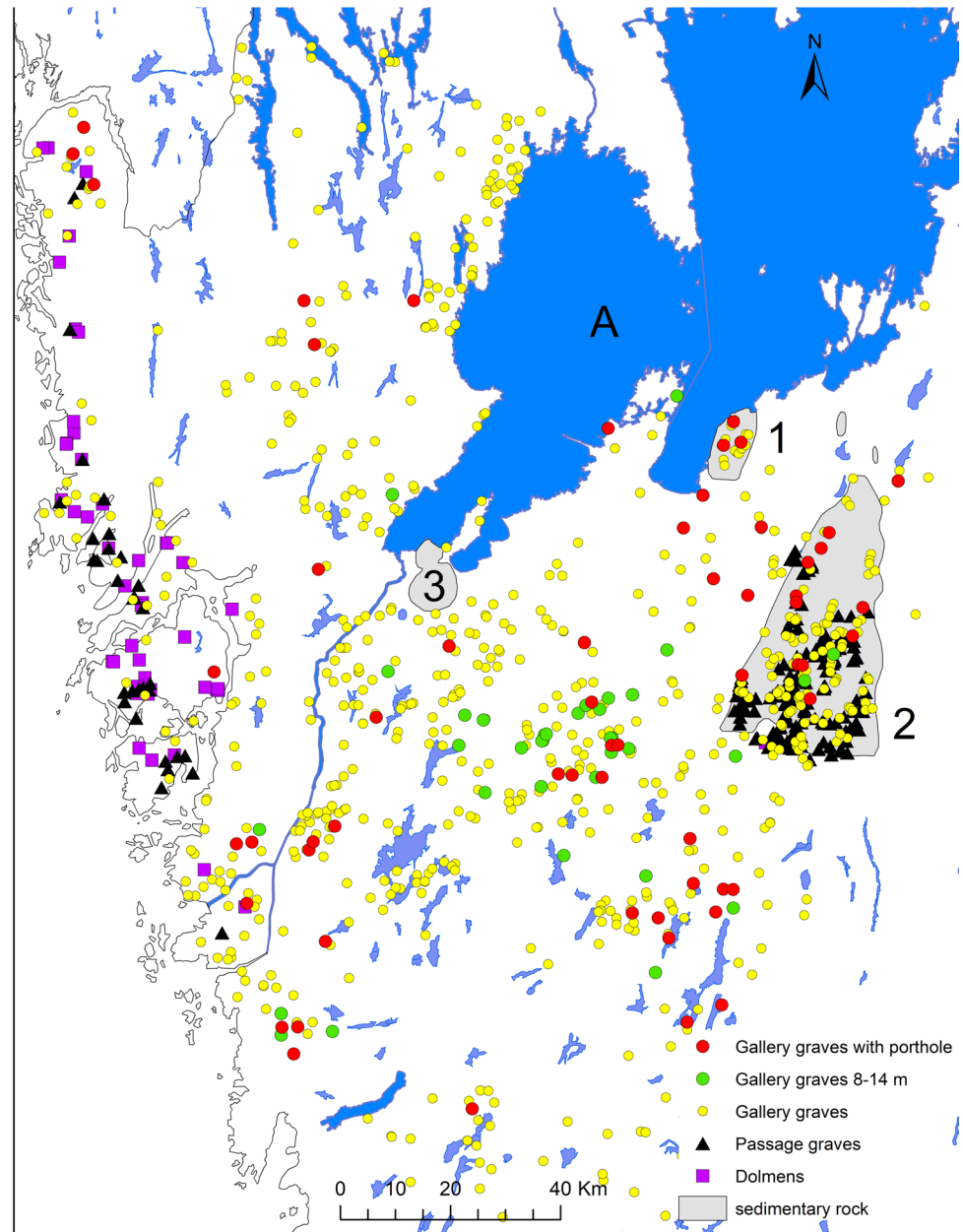
example ax-bearing figures and figures with wings, crooked beaks, and swords (Weiler 1994: 92). Several of the carvings can be dated to the EBA. Close by, several rock art sites consisting of cup marks and foot soles are recorded.

The most prominent prehistoric remains at Kinnekulle are the 20 gallery graves concentrated to the 55 square km large area (Fig. 2). The gallery graves are located on the limestone plateau about 150 masl. They form five groups of equally sized gallery graves (Weiler 1994: 81). The few stray finds consisting of ca. ten flint daggers and shaft-hole

axes may be remnants from destroyed gallery graves. Unlike in Falbygden, the largest sedimentary area in inland southwestern Sweden, no megalithic or flat graves dated to the Early or Middle Neolithic periods are so far known at Kinnekulle.

The three gallery graves included in this study are located on the limestone plateau: Medelplana 18 in the western part about 3 km from lake Vänern, Medelplana 54 in the northern part ca. 2 km from lake Vänern, and Österplana 27 in the eastern part ca. 5 km from lake Vänern (Fig. 2).

Fig. 1 (continued)



## Site descriptions

### Medelplana 54, Helles gallery grave

In 1916, Schnittger (1920) excavated and removed this gallery grave. It was 7.3×2.5 m large and constructed below ground. The grave had slightly curved long sides, similar to the Danish Bøstrup cists and oriented NW- SE, with an ante-chamber in the northwestern part. The walls were constructed by double limestone slabs. The two limestone slabs separating the chamber and ante-chamber were cut into a vague port-hole (Fig. 3).

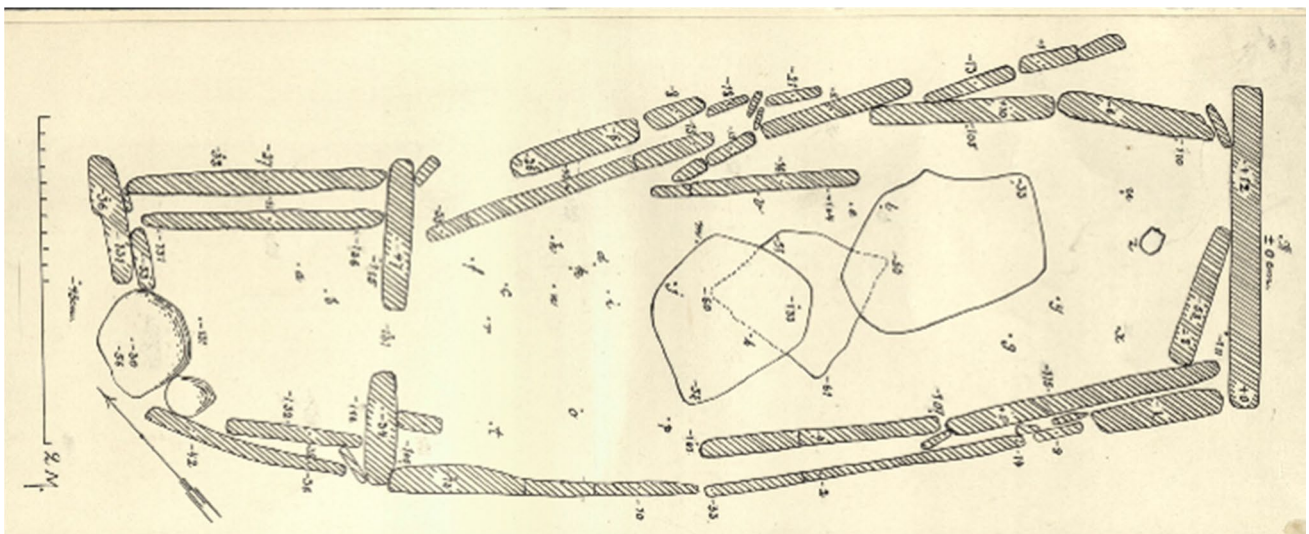
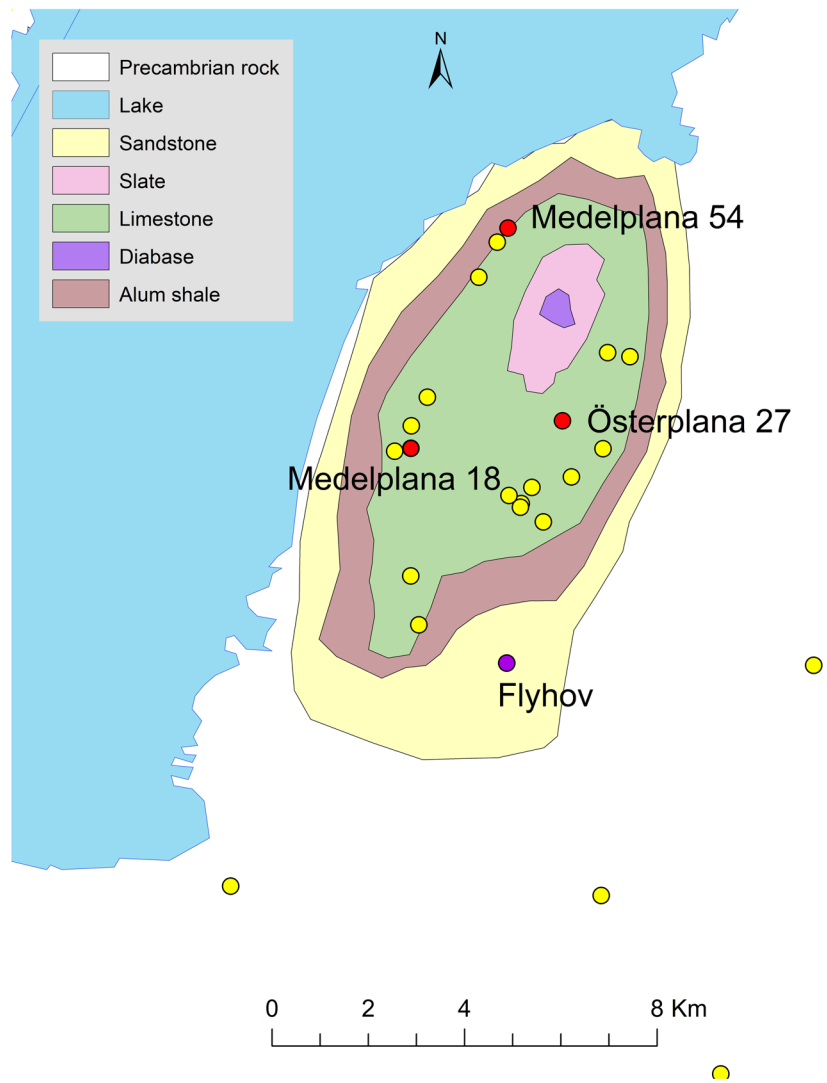
During the excavation, Schnittger (1920) estimated the human remains belonging to about 60 individuals. A

more recent osteological investigation concluded that the minimum number of individuals of the recovered skeletal remains was 20 (Tornberg 2018). The discrepancy can be explained by several factors: an osteologist did not make the first estimation, human remains might have been left at the site, and bones could have been lost.

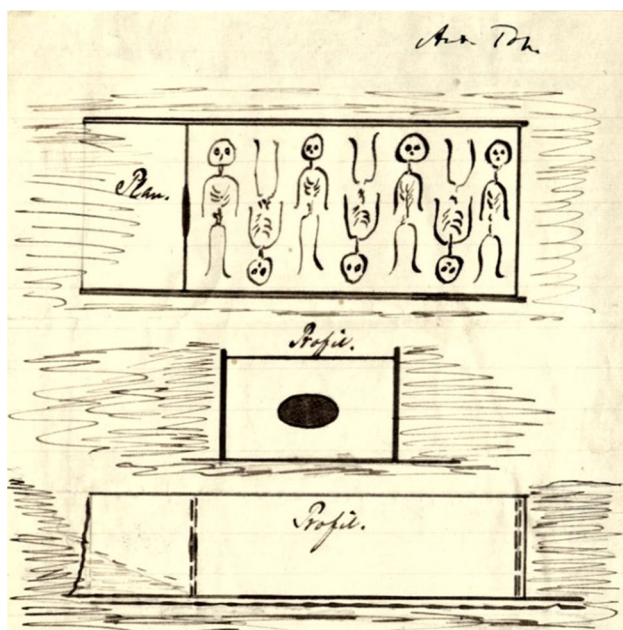
### Österplana 27, Høgebo gallery grave

Nyström (1886) excavated and removed this gallery grave. It was recovered below ground and consisted of a 4×1.4 m large rectangular grave constructed by limestone slabs. The grave was divided by a slab with a circular port-hole into a

**Fig. 2** Overview of Kinnekulle geology with the distribution of gallery graves (yellow dots and red dots the included graves). Purple dot, Flyhov rock art site



**Fig. 3** Plan of the Medelplana 54 gallery grave (Schnittger 1920)



**Fig. 4** Drawing of the Österplana 27 gallery grave (Nyström 1886)

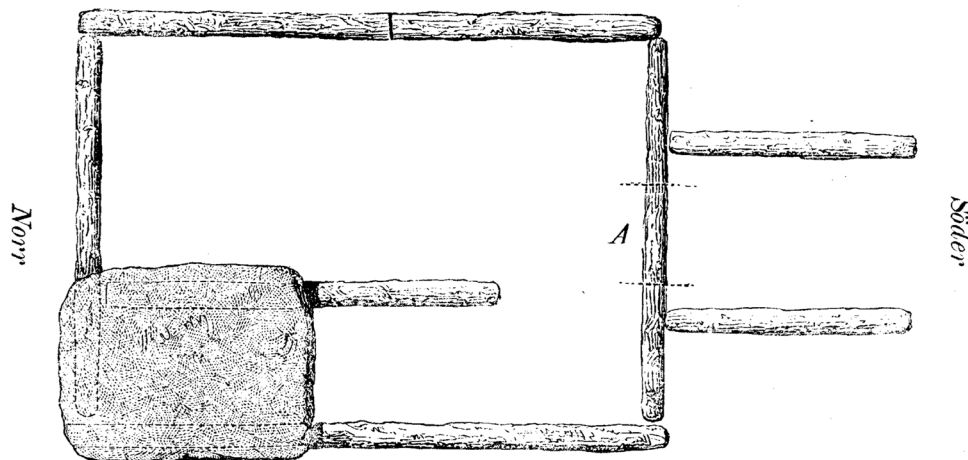
chamber and an open ante-chamber in the west-southwestern end (Fig. 4; Nyström 1886; Sahlström 1915:81).

According to Nyström (1886), skeletal remains from about 50 individuals were found and the partially articulated skeletons were well preserved and placed in sitting positions against the chamber walls. Nevertheless, in his drawing (Fig. 4), the skeletons are placed in supine positions. The illustration cannot be considered to depict an accurate placement of the bones and the description of the sitting position may as well be interpreted as bodies put in a contracted arrangement. Only 25 skulls are stored at the depository at SHM, from this grave.

#### Medelplana 18, Karlsgården

In 1865, this gallery grave was excavated and removed (Montelius 1905). It was found below ground underneath

**Fig. 5** Plan of the Medelplana 18 gallery grave (Montelius 1905)



a small mound surrounded by kerb stones. The grave was 3.3×1.8 m large, oriented N-S, and consisted of a rectangular chamber constructed by four limestone slabs and a short passage narrower than the chamber built with two limestone slabs. In the slab dividing the chamber and the passage, a half-circular port-hole was observed (Fig. 5). These types of port-holes are not so common in Västergötland but appear in several gallery graves in the coastal regions of Bohuslän and Halland (Montelius 1905). Inside the chamber, parallel to the long side, a slab formed a niche, which was partially covered by a roof slab (Fig. 5).

Most of the skeletons were reburied in the chamber after the excavation. However, a femur, a piece of a mandible, and a loose molar tooth were collected and preserved.

#### Material

The recovered artefacts were studied at the Swedish National Historical Museum (SHM) depository, and the documentation of the graves were retrieved from the Antiquarian-Topographic archive (antikvarisk-topografiska arkivet/ATA) along with supplementary information found in Montelius 1905 and Sahlström 1915. The artefacts were typologically dated, and details of the finds and material were registered. We also sampled skeletal remains from the SHM depository at Tumba (see below).

#### Sampling strategy and selection criteria

We sampled the three gallery graves from Kinnekulle where human bones were collected during excavations. Our strategy was to sample as many unique individuals as possible where both enamel and bone for collagen was available. We therefore adjusted the sampling in the specific graves according to the availability of different parts of jawbones with

teeth in situ from the commingled and fragmented skeletal remains. Of the material from the Medelplana 54 and Österplana 27 graves, we sampled teeth in mandibles from unique individuals, while a single loose tooth was analysed from the Medelplana 18 grave. The teeth were primarily targeted to be able to include a variation of isotope and biochemical analyses with only minimal destruction of the human remains. In three cases, mandible bones were sampled for radiocarbon dating and stable isotope as the tooth was used for aDNA and Sr isotope analysis (SI 1). Of the Medelplana 54 and Österplana 27 graves, when possible, we sampled two or three molars from the same individual to be able to detect possible movements during childhood and early adolescence. Only three individuals were sampled from Österplana 27, as we only were allowed to sample teeth or loose bones from the skulls.

We sampled the enamel in bulk instead of measuring it on a micro scale, as this technique was not available for us at the moment of sampling. Enamel mineralization may take several years, which means that the measured Sr isotope ratios of our bulk samples represent an average of the Sr which has been incorporated during this process (Montgomery 2010: 330). We included first (1), second (2), and third (3) molars, with crown formations spanning from 0 to 3 years in M1s, 2.5–8 years in M2s, and 7–16 years in M3s (Nelson and Ash 2010: 31). Second molars were prioritized over third molars, where enamel forms later and over a longer time. In turn, isotope ratios in first molars may be affected by weaning (Fuller et al. 2003).

The isotope ratios in different bone elements represent different ages of the individuals, as the rate of chemical and structural turnover varies. Tooth dentine, as well as the petrous bone (part of the temporal bone), is inert and the isotopic signals thus originate from childhood, although the second and third molars may also reflect the youth (Ubelaker 1989). The roots of the teeth were sampled, which should indicate the average diet over several years. The collagen in other bone elements reflects an average of several years of diet prior to death, due to the rate of turnover. In most cases,

dentine was sampled for radiocarbon dating,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes (SI 1).

## Overview of samples

We sampled 18 individuals from inhumation burials for nitrogen, carbon, and strontium isotopes. Teeth, mostly molars, were sampled to maximize the number of analyses and minimize the destruction of material. Thus, the results reflect the childhood/youth (the root formation and the enamel crystallization) of the individuals. Most of the sampled individuals were found in Medelplana 54 (Table 1). In 11 cases, several teeth of the same individual, representing different ages, were sampled for Sr isotope analysis (three individuals from Österplana 27 and eight from Medelplana 54). In addition, we sampled tooth roots from 17 of these individuals for ancient DNA analyses (aDNA). The radiocarbon dates of all sampled individuals were published in previous studies (Blank et al. 2020; Fibiger et al. 2013) and recalibrated and modelled in this study (see method).

## Method

### Osteology

Sex, age, and paleopathology of adults and non-adults were registered using a standard analytical protocol, when applicable (Buikstra and Ubelaker 1994). Considering the commingling of the skeletons, the remains could not be assessed to specific individuals. A minimum number of individuals (MNI) approach was used to estimate the number of individuals inhumed in the graves. MNI was calculated by the skeletal element (MNE) count with the highest frequency in each context. Side, age, and sex were considered in the estimation. For further information about the osteological registration process, see SI 2.

**Table 1** Included samples from the gallery graves

Site	Medelplana 54		Medelplana 18		Österplana 27		Total	
	No of samples	No of individuals	No of samples	No of individuals	No of samples	No of individuals	No of samples	No of individuals
$^{87}\text{Sr}/^{86}\text{Sr}$ (enamel)	26	13	1	1	7	3	34	17
$\delta^{15}\text{N}$ (collagen)	14	14	1	1	3	3	18	18
$\delta^{13}\text{C}$ (collagen)	14	14	1	1	3	3	18	18
$\delta^{13}\text{C}$ (enamel)	22	13	-	-	7	3	29	16
aDNA	13	13	1	1	3	3	17	17



## Strontium isotopes

Sr isotope analysis has become an established method for studying human and animal mobility (e.g. Frei et al. 2015, 2019; Gron et al. 2016; Knipper 2011; Knipper et al. 2017; Montgomery and Evans 2006; Price et al. 2004; Sealy et al. 1995; Sjögren and Price 2013; Snoeck et al. 2020). For more detailed information on Sr isotopes, see (Bentley 2006; Faure 1986; Montgomery 2010; SI 2).

We used the Sr isotope baseline published in Blank et al. (2018b). The baseline was constructed by isotope ratios of 89 samples from water and small non-domestic fauna from locations with various geological characteristics in Västergötland (Blank et al. 2018b). The Sr isotope range between 0.714 and 0.719 is here referred to as “Local”, as this span occurs within Kinnekulle (Fig. 6). However, this range partly overlaps with the ranges of other sedimentary areas within the region as well as terrains south of Falbygden (Fig. 6). According to the interpolated surface model, the Sr isotope ratios where the gallery graves are found ranges from 0.714 to 0.717 (Fig. 6). In the surrounding Precambrian areas ratios between 0.719 and 0.726 are found, which we consider “Non-local within VG”. Higher ratios appear east and north-east of Kinnekulle (Fig. 6; Åberg 1995; Åberg and Wickman 1987; Löfvendahl et al. 1990). Thus, Sr isotope ratios above 0.726 are referred to as “Non-local outside VG”, as are Sr isotope ratios below 0.712. Sr isotope ratios below 0.712 are not found in Västergötland but have been recorded in Scania, in Denmark, at Öland and in coastal areas such as

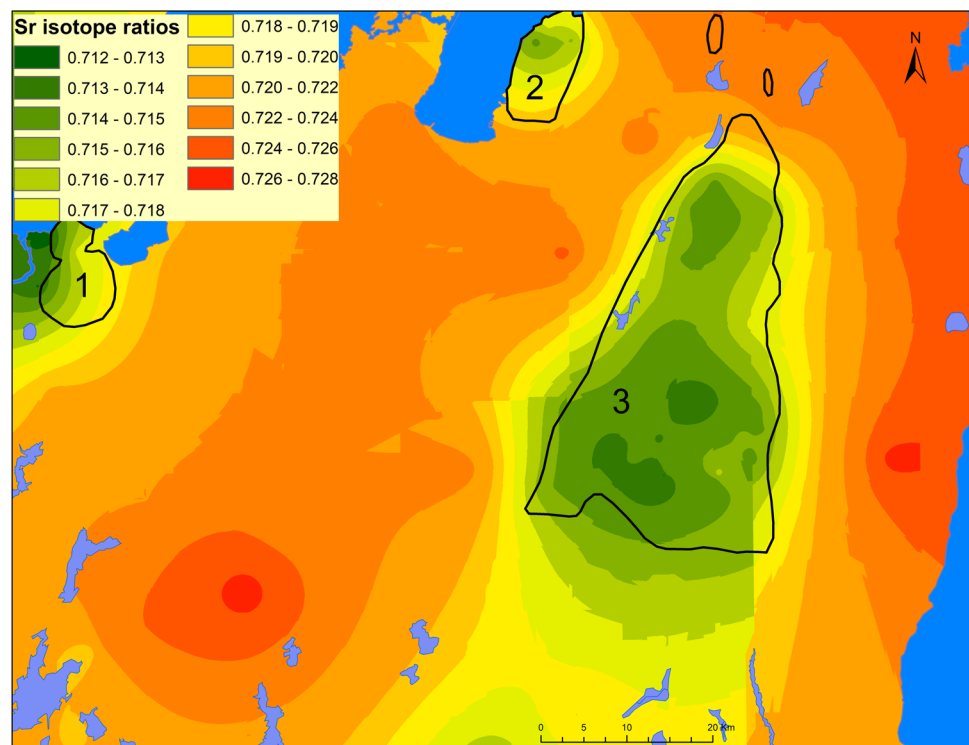
the Swedish west coast and further away (Arcini et al. 2016; Bergerbrant et al. 2017; Fornander et al. 2015; Fraser 2018: 61; Frei and Frei 2011; Frei and Price 2012; Klassen et al. 2020; Oras et al. 2016; Sjögren et al. 2009; Wilhelmson and Ahlström 2015).

Enamel sample preparation and strontium isotope analysis were carried out at the Curt Engelhorn Center for Archaeometry in Mannheim, Germany following Knipper et al. (2012) and at the Danish Center for Isotope Geology, University of Copenhagen, Denmark by Karin M Frei and Robert Frei. A blind test was performed in a previous study and the difference between the results from the same tooth obtained at the two laboratories was  $<0.0001$  (Blank et al. 2021). For more details on the preparations and analyses, see SI 2.

## Carbon and nitrogen isotopes

Stable isotope analysis of human collagen is a recognized method of estimating general consumption patterns and subsistence. Analyses of  $\delta^{13}\text{C}$  can be used to distinguish terrestrial from marine diets (Sealy 1986). In the Atlantic/North Sea region, terrestrial mammals have  $\delta^{13}\text{C}$  end values of bone collagen ranging from  $-20$  to  $-21\text{‰}$ , whereas the marine end value is about  $-10\text{‰}$  (e.g. Barrett et al. 2011; Fischer et al. 2007). Intermediate  $\delta^{13}\text{C}$  would thus reflect a combination of marine and terrestrial proteins. Furthermore, consumers of freshwater and marine fish, and other aquatic predators have higher  $\delta^{15}\text{N}$  values, up to  $15\text{‰}$  or even  $20\text{‰}$ ,

**Fig. 6** An interpolated surface area of Sr isotope ratios based on data from Blank et al. (2018a). 1: Halle and Hunne mountains, 2: Kinnekulle, and 3: Falbygden



as aquatic food webs have generally longer food chains than land-based webs (Schoeninger et al. 1983: 130). The  $\delta^{15}\text{N}$  values increase along the food web, although different fractional levels have been suggested ranging between 3 and 6‰ per trophic level (e.g. Ambrose 2000; Bocherens and Drucker 2003; DeNiro and Epstein 1981; Hedges and Reynard 2007; O'Connell et al. 2012). Thus, the interpretation of the origin of the protein might differ depending on which fractionation level is considered. The enrichment of stable isotopes and reservoir effects are further discussed in SI 2.

Reference samples from LN and EBA fauna and flora are few and therefore no quantitative dietary reconstructions were performed. However, the stable isotope analyses of both collagen and enamel enable us to get a relatively good idea of the general diet, as bone collagen mainly reflects protein intake, while bone and enamel carbonate (apatite) mirrors overall dietary components (protein, carbohydrates, and fats). Furthermore, the difference between the  $\delta^{13}\text{C}$  in apatite and the  $\delta^{13}\text{C}$  in collagen (the collagen-apatite spacing) observed in carnivores is smaller than in herbivores (Ambrose and Norr 1993; O'Connell and Hedges 2017). The collagen-apatite spacings are  $6.8 \pm 1.4\text{‰}$  for herbivores,  $5.2 \pm 0.8\text{‰}$  for omnivores, and  $4.3 \pm 1.0\text{‰}$  for carnivores (Hedges and Van Klinken 2002; Lee-Thorpe et al. 1989; O'Connell and Hedges 2017).

Analyses of stable carbon and nitrogen isotopes in collagen were conducted at the  $^{14}\text{C}$ Chrono Centre, Queens University, Belfast. The stable carbon isotope analyses of bioapatite were performed at the Institute of Geosciences, Department of Applied and Analytical Palaeontology at the University of Mainz, Germany. Methods of sample preparation and isotope analyses are described in the SI 2.

### Biomolecular analysis

Ancient DNA from human remains can provide information concerning biological sex, genetic inheritance, biological kinship relations, population history, and diseases (Bramanti 2013). This study includes sex assessments and reports mitochondrial (mtDNA) haplogroups. The mtDNA can only be passed on by the mother to an offspring and can be used to establish relatedness on the maternal side. Haplotypes are a combination of sequence variants derived via mutations from an ancestral sequence. Haplotypes which have a similar origin can be arranged in haplogroups (Bramanti 2013).

All aDNA analyses were performed at Uppsala University. DNA extraction and library preparation were conducted in a clean room laboratory dedicated to ancient DNA work. Illumina shotgun sequencing was performed at SciLife SNP&SEQ platform. Bioinformatic data processing was computed using the resources of Uppsala Multidisciplinary Center for Advanced Computational Science (UPPMAX). DNA extraction and library preparation, shotgun sequencing, data processing, and analyses of mtDNA haplogroups

and genetic sex assessments were conducted as presented in Blank et al. (2021).

### Statistical analyses

The data evaluation included descriptive statistics, correlation, and significance tests. The non-parametric Mann–Whitney *U*-test was used to examine whether the observed differences were statistically significant at the 5% level. This test was favoured because of the non-normal distribution of values. Furthermore, statistical methods such as Bayesian and KDE models were included, described in SI 2. The calibrations, plots, and models of the radiocarbon dates were conducted using the OxCal online software version 4.4.4 (Bronk Ramsey 2021, Bronk Ramsey 2009) and the IntCal20 atmospheric curve (Reimer et al. 2020).

## Results

### Artefacts

The artefacts recovered from the gallery graves mainly consist of common objects found in LN gallery graves throughout Scandinavia (Anderbjörk 1932; Ebbesen 2007; Østmo 2011; Weiler 1994). However, in two graves (Medelplana 54 and Österplana 27), flint artefacts (a tanged blade arrowhead and a thin bladed polished flint axe) dating to the MN were found (Table 2). A now lost shaft-hole axe has been reported from Österplana 27 (Nyström 1886).

The majority of the artefacts consist of flint objects (Table 2). Most of these were produced from imported south Scandinavian flint from Denmark and Scania, although in the Medelplana 54 grave, two of the arrowheads were made of local Cambrian flint from Kinnekulle. Nine flint daggers were recovered in the graves and all of them were of late types (IV–V) according to Lomborg's (1975) typology. The two daggers of unknown type in Medelplana 54 might be of type VI but may also be of earlier types. At least two of the daggers had been used as strike-a-lights.

Slate pendants were recovered in two of the graves and part of a flint sickle in Medelplana 54. According to a previous study of artefacts in gallery graves in inland southwestern Sweden (Blank 2022), both these types of artefacts can be dated to the later part of LN or EBA. Bone needles, which were found in Österplana 27, are common objects in gallery graves and primarily interpreted as dress pins. Bone artefacts may have been overlooked during excavation as much of the skeletal remains were left or reburied at the sites. No amber artefacts were recovered.

**Table 2** Compilation of artefacts, based on Blank et al. (2020) and Schnittger (1920). Daggers were classified to type (I–VI) according to Lomborg (1975)

Site and inventory number	Flint	Bone	Slate	Pottery
	Daggers	Arrowheads	Other	Needles Pendants Vessels
Medelplana 54 SHM 15 660	6 (2×?, 2×IV, 2×V)	1 tanged blade arrowhead, 6 bifacial arrowheads with concave bases.	1 sickle, flakes, scrapers, bifacial arrowhead preform	4 3 (two undecorated and one covered with stamp decoration)
Medelplana 18 SHM 3482	1 type V			1
Österplana 27 SHM 7881, 15 944	2 (1×IV and 1×?)		1 thin bladed polished axe, bifacial arrow- head preform	5
Total	9 (3×?, 3×IV, 3×V)	1 tanged blade arrowhead, 6 bifacial arrowheads with concave bases	1 sickle, 1 axe, scrapers, flakes, bifacial arrow- head preforms	5 5 3

## Osteology and genetic sex assessments

### Medelplana 54

A minimum number of 20 individuals, 17 adults, and three juveniles were osteologically analysed. The skeletal remains were commingled, but the remains consisted of at least six males and eight females, when only osteological estimates were considered. A subset of the individuals was sampled for aDNA ( $N=13$ ) and 11 of them could be genetically sex assessed (SI 1, 2). The six males determined morphologically were confirmed to be genetic males also. Two morphologically undetermined adults were also shown to be genetic males. Furthermore, one individual (MM4) was estimated as a probable female based on the morphology of the mandible, but the DNA analysis provided a male sex, giving a total of nine males within the tomb. Two individuals that could not be osteologically assessed for sex were determined as females through aDNA (MM8 and MM12). Both females were aged as over 20 years. Unfortunately, only a subset of the osteologically assessed female individuals could be sampled for chemical analyses due to the lack of jaws with teeth in situ. One or more of the mandibles with undetermined sex could be linked to females that were morphologically assessed through traits of the pelvis or cranium, which is why the MNI count does not increase with the genetically assessed females.

All males were possible to assess with age: 17–25 years ( $N=2$ ), 25–35 years ( $N=3$ ), and 35–45 years ( $N=1$ ), as well as one individual under the age of 20 years and two individuals over 20 years. It should be noted, however, that dental attrition is closely connected to cultural behaviour such as

diet and the use of teeth as tools, and the estimates should therefore be considered tentative only. Three children were identified: 3–5 years, 7–9 years, and 10–12 years, according to tooth development.

The frequency of dental caries could be calculated from 159 scorable post canine permanent teeth, both in situ in the jaws and loose teeth. Eleven of the teeth showed some sort of carious lesions, with the majority situated interproximal on the molars. This corresponds to a frequency of 6.9%. Only three deciduous molars could be analysed, none of them exhibiting carious lesions.

Signs of general physiological stress were evident both as *cribra orbitalia* (CO) and linear enamel hypoplasias (LEH). CO was detected in 7/28 (25%) of the examined orbits (both left and right), most of them showing signs of healing. LEH could be registered in 24/212 (11.3%) of the permanent teeth. None of the deciduous teeth showed signs of LEH.

Noteworthy is that the number of traumatic injuries is relatively high considering the limited number of individuals. Most injuries were probably caused by accidents. A total number of 11 elements showed signs of trauma, out of which nine showed evidence of some, or extensive, healing. Two of the injuries (skull traumas) are so poorly preserved that post-mortem damage cannot be ruled out. Fibiger et al. (2013) provide information of one perimortem fracture on the left parietal of a male, which may correspond to one of these uncertain peri-/post mortem traumata. The healed traumata include two left femoral neck fractures, one of which may be associated to a trauma on the left ilium. Six other traumas were found: another iliac fracture (which might be the same individual as the other femoral neck fracture but this cannot be definitely concluded), one fracture of a left twelfth rib, one fractured first finger phalange, one fracture of the styloid process of a left ulna, a fractured left orbit of a female, and a

fractured left lower jaw of a male. It is possible that the two skull traumata are related to violent acts.

Lastly, one individual showed evidence of significant erosive lesions of the endocranial surface of the occipital. These types of lesions are generally considered to be caused by haemorrhage or inflammation of the meningitis, but the reason could be multicausal, such as, e.g. tuberculosis, trauma, vitamin deficiency, and tumours (Lewis 2004). Unfortunately, it is not possible to link this cranium with any of the individuals sampled for isotope analysis due to the commingled state of the remains.

### Österplana 27

From Österplana 27, skulls from a minimum number of 25 individuals were osteologically analysed. The skulls correspond to 19 adults and 6 subadults, with the sexes among the adults equally distributed (8 females, 9 males, and 2 adults of indeterminate sex). The individuals that were sampled for isotope analyses were all males (SI 1, 2), two of them in their late teens or young twenties, and one in his older twenties or early thirties. aDNA data from three of the osteologically determined males confirms that they were also genetic males (SI 1, 2).

Since only skulls were available for analysis, the osteological data is sparse and only include evidence of pathological conditions of the head region, which is of course affecting interpretations on health. Particularly interesting is evidence of violence. Out of the 19 adult skulls, two (10.5 %) show evidence of trauma, both ante-mortem and peri-mortem. The presence links to the general increased trend of skull traumata seen in LN-EBA southern Sweden (Tornberg 2022). One of each sex was affected. The female, an older adult, has an almost completely circular, 23.3×23.4 mm, healed fracture above the right orbit. She also has a button osteoma, i.e. a benign bone tumour, at the midline of the frontal bone. Lastly, the female also exhibits a peri-mortem, blunt force fracture on the margin between the right frontal and parietal bones. It is evident that the individual suffered from at least two violent events throughout her lifetime, one of which was probably the cause of death. The button osteoma should not have caused any health problems for the individual. The other cranium is from a male that seems to have died a violent death, with a peri-mortem fracture visible on his left frontal.

Only three individuals, a young male and two subadults, showed evidence of general stress in the form of cribra orbitalia. The individuals were not chosen for dating and isotope analyses.

Noteworthy is the high occurrence (8/25 individuals) of extra sutural bones/ossicles, i.e. a non-metric skeletal trait, in the material. Sagittal, lambdoid, and apical ossicles are

all present. Individuals of both sexes (1 male, 3 females, 2 indetermined, 2 subadults) express ossicles of some sort. It is possible, however far from conclusive, that these traits correspond to genetic affinity (Larsen 2015; Konigsberg et al. 1993; Sjøvold 1984).

### Medelplana 18

The osteological material from the Medelplana 18 gallery grave was only represented by a right mandible with pre-molars and molars in situ, a right proximal femur from an adult, and a loose upper left first molar. The loose first molar was sampled for biochemical analyses (see above). There are no clear morphological traits for sex estimations. However, the mandible exhibits more masculine than feminine characters, and the dimension of the femoral head is suggestive of male sex. Thus, the sex estimations are to be considered tentative only. However, the loose molar tooth belonged to a female according to sex assessment based on aDNA (SI 1). The teeth in the mandible are heavily worn, indicative of an age between 35 and 45 years, using Brothwell's (Brothwell 1981) model. The upper first molar has a wear pattern in accordance with an age of 25–35 years, thus probably not from the same individual as the mandible. As such, the minimum number of individuals remaining from Medelplana 18 is two. However, as already mentioned, the grave contained many more individuals but most of the recovered skeletons were reburied after the excavation.

### mtDNA haplogroups

In general, the samples displayed the properties expected for ancient DNA data. The average read length ranged from 50 to 82 base pairs, and ratios of C to T and G to A damages at the ends of the reads ranging from 0.10 to 0.37. Mitochondrial aDNA haplogroups were determined for 7 individuals in Medelplana 54 and from one individual in Österplana 27 (SI 1, Table 3). The eight individuals that yielded mtDNA data all displayed unique haplotypes. The mtDNA haplogroups are presented in Table 3 and in Fig. 7 is the distribution of simplified mtDNA haplogroups over time.

### Radiocarbon dates and burial sequences

In this study, the radiocarbon dates, which previously were part of a compilation study of 215 <sup>14</sup>C dates from Swedish megalithic graves (Blank et al. 2020), were recalibrated and used for discussing and modelling the use time of these specific graves. The collagen quality of the all 18 samples was acceptable with C:N atomic values ranging between 3.14 and 3.31 (SI 1, Bronk Ramsey et al. 2004; Van Klinken 1999). There were no signs of freshwater or marine reservoir

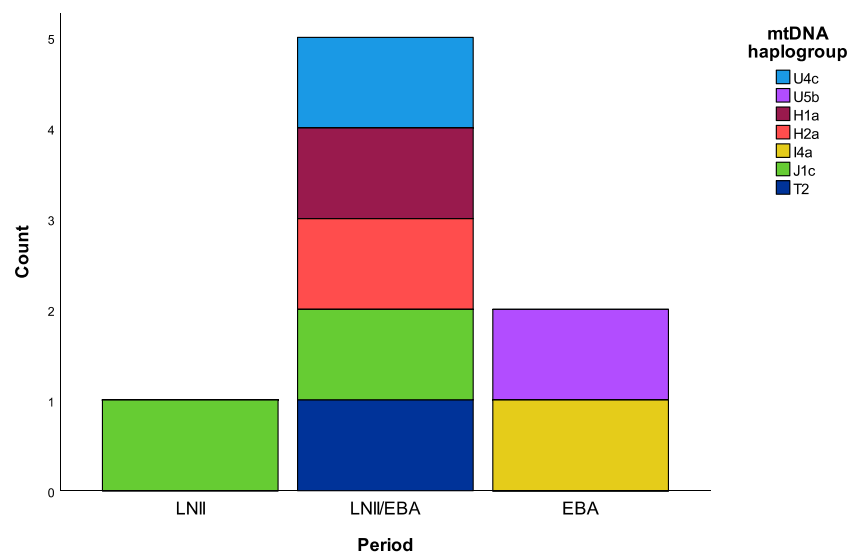
**Table 3** Distribution of mtDNA haplogroups and sex assessments of sampled individuals in the three gallery graves. M, male; F, female; N.D, not determined; LN, Late Neolithic; LN/EBA, transition between the Late Neolithic and Early Bronze Age; EBA, Early Bronze Age

Site	Ind. No.	Period	Sex (genetic-osteological)	mtDNA haplogroups
Medelplana 54	MM1	LN/EBA	XY-N.D	N.D
	MM2	EBA	XY-M	N.D
	MM3	LN/EBA	XY-M	U4c1a
	MM4	EBA	XY-F?	U5b2a1a1
	MM5	LN/EBA	XY-M	N.D
	MM6	LN/EBA	XY-M	H2a
	MM7	EBA	XY-M	I4a
	MM8	LN/EBA	XX-N.D	J1c7
	MM9	LN II	N.D-N.D	N.D
	MM10	LN/EBA	XY-N.D	N.D
	MM11	LN/EBA	N.D-N-D	N.D
	MM12	LN/EBA	XX-N.D	H1a3
	MM13	LNII	XY-N.D	J1c8a
Österplana 27	MP1	LN/EBA	XY-M	N.D
	MP2	LN/EBA	XY-M	T2
	MP3	EN/MN	XY-M	N.D
Medelplana 18	KM1	LN/EBA	XX-N.D	N.D

effect, with regard to the stable isotopes and collagen apatite-spacing (see Carbon and nitrogen isotopes in SI 2), and the typological dates of the related finds (see “Artefacts”).

In Fig. 8, the 18 radiocarbon dates are presented in a sum plot. One of the individuals is dated to ca. 3500–3100 BC, 95.4%, while the remaining burials range ca. 1900–1490 BC, 95.4%.

**Fig. 7** Stacked bar chart of simplified mtDNA haplogroups of individuals buried in gallery graves in at Kinnekulle. LN, Late Neolithic; LN/EBA, transition between the Late Neolithic and Early Bronze Age; EBA, Early Bronze Age



### Medelplana 54

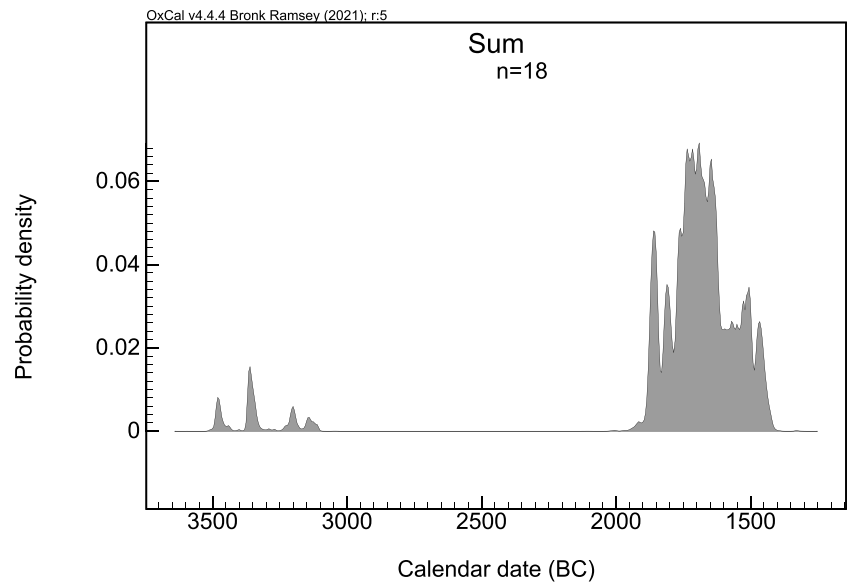
The fourteen sampled individuals from this grave were dated to an interval spanning from the LN II to the EBA period II (1889–1442 BC, 95.4%) (SI 1). According to the sum plot, most of the radiocarbon dates fall in the transition between LNII and EBA. Two burials can be dated to the LNII and three burials to the EBA period I/II (Fig. 9). The sum plot suggests a use time of the grave of about 460 years.

We produced two statistical models of the radiocarbon dates (a Bayesian and a KDE model) to investigate the time of use further. However, we are dealing with data lacking reliable prior information as the dates derives from commingled skeletons without stratigraphic information. So, in this case, we must assume the priors. In the Bayesian approach, the events are in one or another way compressed, depending on the chosen model (see statistical models in SI 2). The model with the best fit according to the agreement indexes is presented here, which is a model based on one single phase where the events are assumed to be randomly sampled from a uniform distribution (Fig. 10).

In this model, the dates span from the LNII to EBA period I, with most dates concentrated to the transition between LNII and EBA. As the dates are compressed towards the centre, the estimated time of use appears shorter than in the sum plot, suggesting 220 to 330 years of burial activity (1832–1683 to 1649–1499 BC, 95.4% and 1779–1709 to 1626–1555 BC, 68.3%).

KDE model is a non-parametric method of kernel density estimation and can be described as a mixture of the Bayesian and frequentist methods. According to this model, the dates span from the LNII to the EBA period II, with a peak in the LNII (Fig. 11). Here, the time of use was estimated between 300 and 400 years (1856–1687 to 1622–1448 BC, 95.4% and 1781–1694 to 1614–1486 BC, 68.3%). We would consider

**Fig. 8** A sum plot of <sup>14</sup>C dates for all sampled individuals from the three gallery graves

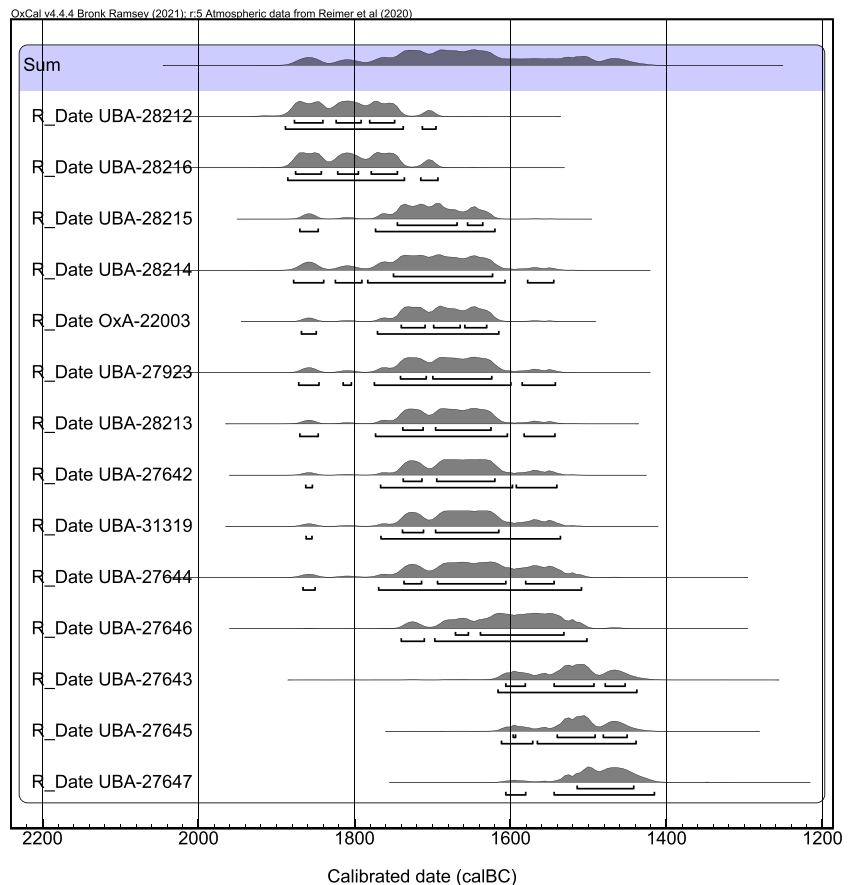


this model relatively reliable if the total number of burials was 20, and not 60 (see “Site description”).

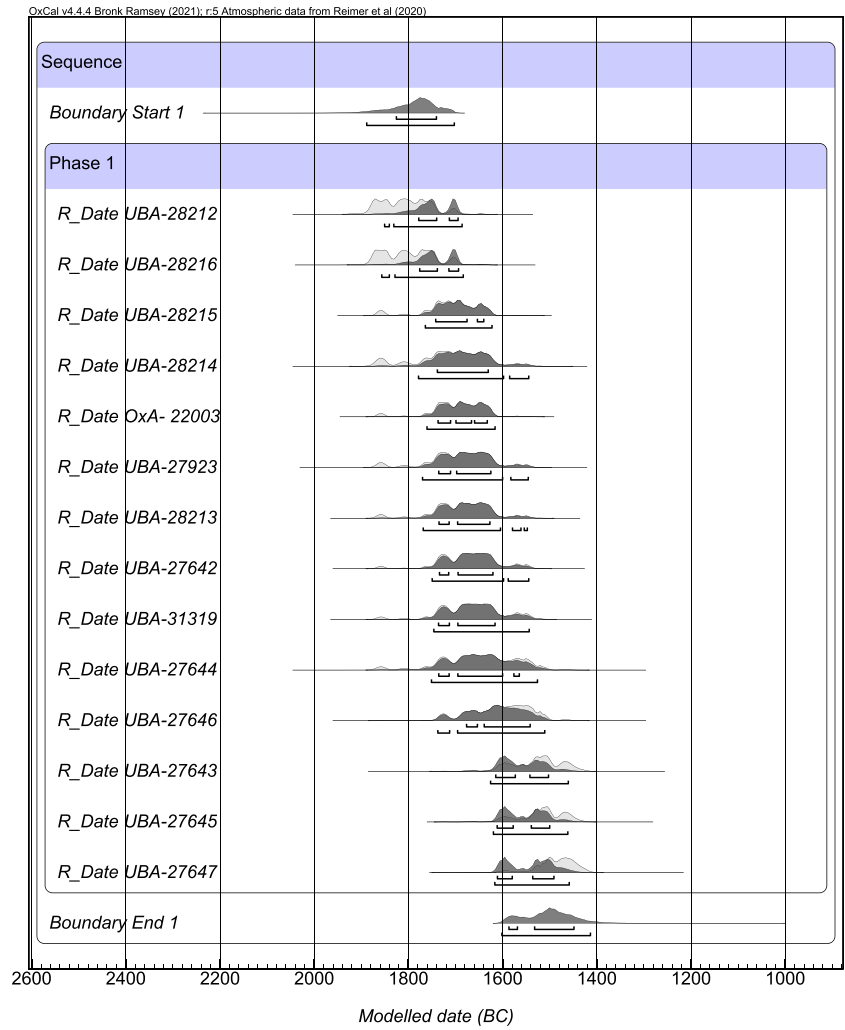
If the number of inhumations were 20 in 300 years, we can assume that an average of ca. 1.7 individuals was buried

per generation (25 years). In the scenario of 60 inhumations, the number of buried individuals would instead be five burials per generation, although the use time of the grave may in this case not be reliable.

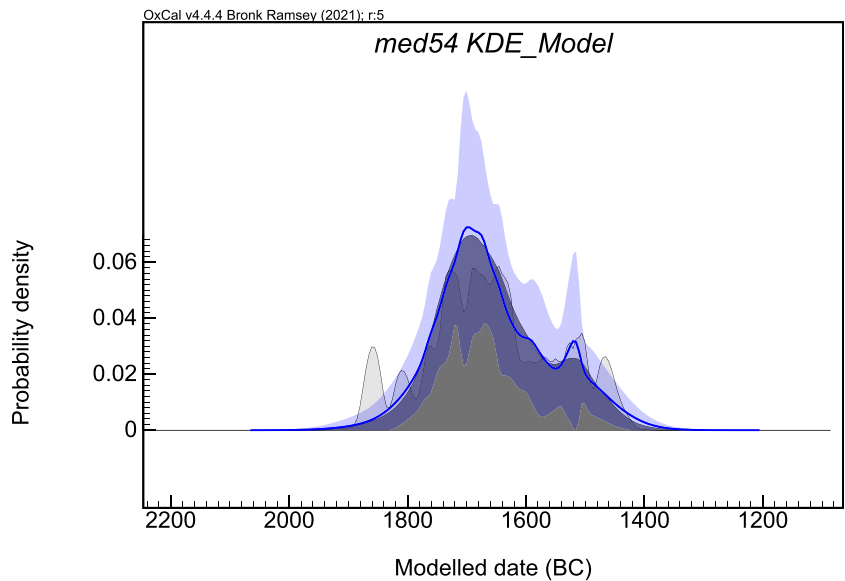
**Fig. 9** Individual radiocarbon dates and a sum plot from Medelplana 54. The individual dates are shown with 95.4 and 68.3% probability spans



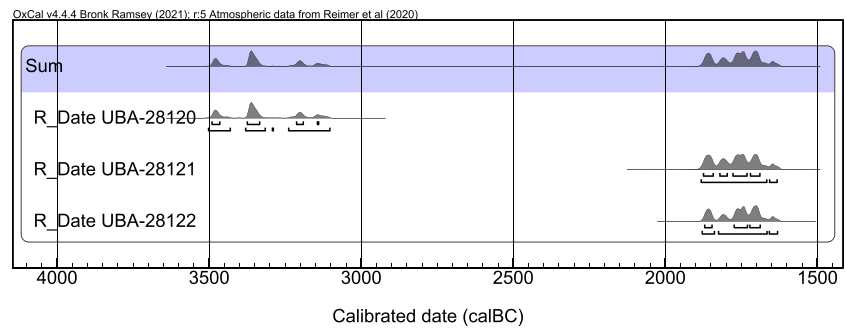
**Fig. 10** Bayesian model with one single phase (boundary) of radiocarbon dates from Medelplana 54.  $A_{\text{model}}=96.8\%$  and  $A_{\text{overall}}=96.3\%$



**Fig. 11** KDE model of radiocarbon dates from Medelplana 54



**Fig. 12** Individual radiocarbon dates from Österplana 27. The individual dates are shown by 95.4% and 68.3% probability spans



## Österplana 27

Two individuals from Österplana 27 gallery grave were dated to the LN II-EBA, between 1884 and 1664 BC (95.4%) while one individual was dated to 3500–3109 BC (95.4%, Fig. 12), covering the end of the EN and the beginning of the MN periods.

Thus, the radiocarbon dates indicate two phases of use, one in the transition between the EN and MN and another in the transition between LN and EBA. However, alternative explanations such as the reburial of an old skull in a LN/EBA grave are also possible. As the number of burials is at least 25 (see above) or originally even about 50 burials as suggested by Nyström (1886), three individuals cannot reliably reflect the burial sequence.

### Strontium isotope ratios

Strontium isotope ratios from enamel of 34 teeth from 17 individuals ranged from 0.711 to 0.736. A few gaps can be observed, where no samples occur, such as 0.712 to 0.714, 0.723 to 0.725, and 0.731 to 0.733. The Sr isotope ratios are similarly spread between the different tooth types (Fig. 13).

Interestingly, most of the samples ( $N=28$ , 71%) fall outside the local range of Kinnekulle (Table 4). Of these, 18 samples (53%) display Sr isotope ratios that according to current knowledge are only found outside of the Västergötland region. A first and a second molar from the same individual exhibit relatively low Sr isotope ratios (0.711). Such ratios are not found in Västergötland and the closest locations where these ratios have been recorded are the Swedish west coast, Scania, and Denmark (see method). At the other end of the scale, 16 samples from 10 individuals have Sr isotope ratios above 0.726, which occur to the east and northeast of Västergötland (see method).

If the number of individuals with different origin is calculated, two individuals only yielded Sr isotope ratios within the local range, while 15 displayed ratios non-local to Kinnekulle (Table 4). The three individuals from Österplana 27 all exhibited non-local ratios from outside Västergötland (Fig. 14).

Some chronological differences can be observed in the mobility patterns (Fig. 14). The two lowest Sr isotope ratios (ca. 0.711) belong to the earliest dated individual (EN/MN) and also the only individual preceding the LN. Furthermore, the highest Sr isotope ratios, above 0.732, were measured in enamel from individuals dated to the transition between the LNII and EBA. According to the Sr isotope data from the LN-EBA individuals, at least three different areas of origin can be assumed (Fig. 14).

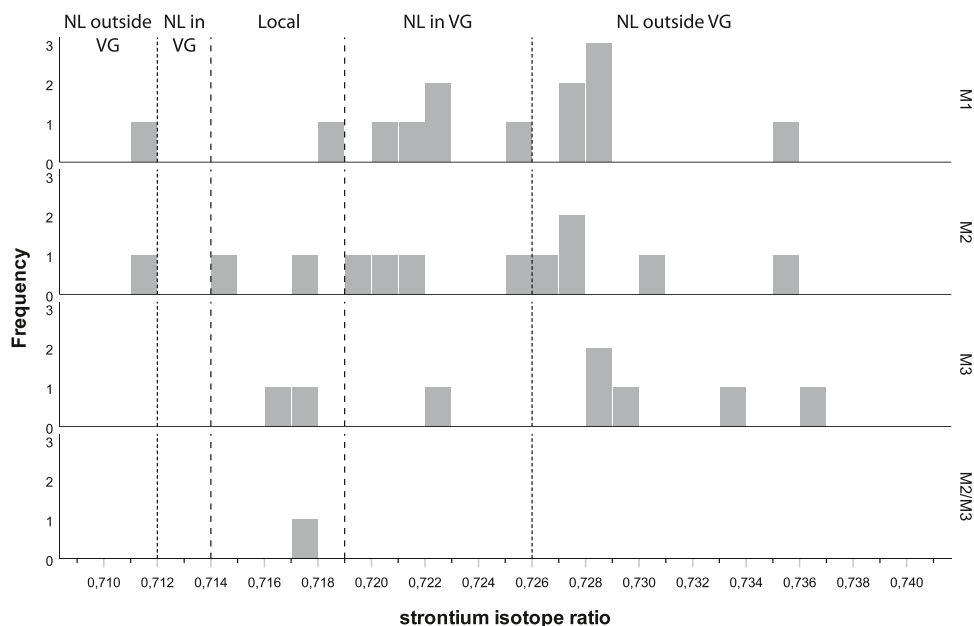
There are some slight but not statistically significant variations between sites, with the highest values observed in the samples from Medelplana 54, and the lowest in Österplana 27 (Mann–Whitney  $U$  test  $p=0.531$ ). The proportion of samples within the local range is low and in Österplana 27, no samples fall within this range (Fig. 14). However, the uneven distribution of samples may affect the results.

In Medelplana 54, the Sr isotopes range from 0.718 to 0.736 and only two individuals (five teeth) have ratios within the Kinnekulle local range. Five individuals exhibit  $^{87}\text{Sr}/^{86}\text{Sr}$  between 0.719 and 0.726, which can be found in the surrounding area of Kinnekulle, while eight individuals display even higher ratios which are found further away, possibly in a more north-eastern direction. In Österplana 27, the ratios range between 0.711 and 0.732. All three sampled individuals displayed non-local ratios which most likely originate from outside VG. The single individual from Medelplana 18 exhibits a ratio local to Kinnekulle (Fig. 14).

In the individuals where several teeth were sampled, individual movements could be observed (Fig. 14). At Österplana 27, the Sr isotope ratios of the EN-MN adult individual MP3 indicate that this person spent his early childhood in an area with relatively low ratios, possibly at the Swedish west coast, in Scania or in Denmark. The ratio of the third molar of the same individual indicates that he moved to more radiogenic terrains that can be found within Västergötland, at the age of 7 to 16 years, whereafter he moved to Kinnekulle or was transported there after death. The two other men from Österplana 27 (MP1, MP2) showed Sr isotope ratios suggesting movements outside of Kinnekulle (in VG and in more eastern/northeastern regions) during childhood (Fig. 14). MP1 has moved to a more radiogenic terrain



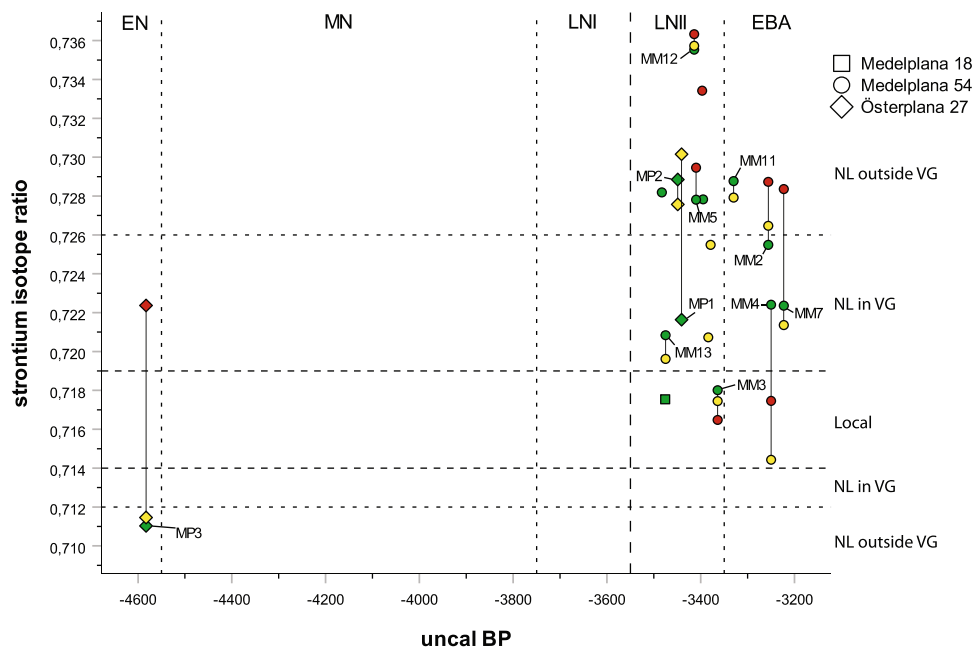
**Fig. 13** Histogram of all samples grouped by tooth type. Dashed lines mark the various mobility ranges. NL, non-local; VG, Västergötland



**Table 4** Samples divided by Sr isotope ranges of the baseline of inland southwestern Sweden (Blank et al. 2018b)

	Local ratios (0.714 to 0.719)	Non-local ratios within VG (0.719–0.726)	Non-local ratios outside VG ( $\leq 0.712$ and $\geq 0.726$ )
Number of samples	6	10	18
% of samples	ca. 18	ca. 29	ca. 53
Number of individuals	2	4	11
% of individuals	ca. 12	ca. 23	ca. 65

**Fig. 14** Scatterplot of Sr isotope ratios and radiocarbon dates of samples from different sites. The lines link the samples from the same individuals. Tooth types are indicated by colour. Green, first molars; yellow, second molars; and red, third molars. EN, Early Neolithic; MN, Middle Neolithic; LN, Late Neolithic; NL, non-local; VG, Västergötland



during childhood while MP2 seems to have remained stationary during his early life. These people may have moved into Kinnekulle sometime after the age of ca. 8 years or could have been brought there only to be buried.

In Medelplana 54, one individual (MM3) seems to have spent his childhood at Kinnekulle or other locations with similar Sr isotope ratios. In the individual MM4 (an adult male), the ratios of the different teeth indicate a move from the Precambrian surrounding areas into Kinnekulle at an age of 3 to 8 years (Fig. 14). Both of these individuals display Sr isotope ratios in their later forming molars estimated in the proximity to the grave sites (0.714–0.717). The remaining six individuals exhibit non-local Sr isotope ratios in all their sampled teeth. Five of them display non-local ratios from outside VG in at least one tooth. Two individuals display non-local ratios found within VG in the early forming teeth and non-local ratios from outside VG in the third molars. Three display non-local ratios from outside VG in all teeth. Thus, movements in the surrounding areas of Kinnekulle and from areas further to the northeast during childhood and early youth are suggested. Furthermore, four of the six individuals only displaying non-local ratios indicate that they could not have moved to Kinnekulle before the age of ca. 16 (MM2, MM7, MM11, MM12). The other two (MM5, MM13) might have moved to Kinnekulle after the age of ca. 8 years (Fig. 14). However, the bodies or even specific skeletal elements only might have been brought to the area after the time of death to be buried.

## Nitrogen and carbon isotopes

### The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in collagen

We obtained stable isotope data of collagen from 18 individuals. The  $\delta^{15}\text{N}$  values ranged between 9.1 and 13.3‰ and the  $\delta^{13}\text{C}$  values between –21 and –19.5‰. In Table 5, summary statistics of the stable isotopes in collagen are presented. The mean values of both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  more or less remain the same regardless of inclusion of the EN/MN sample or not (Table 5). However, there is a difference

**Table 5** Summary statistics of the stable isotopes in collagen

	$\delta^{13}\text{C}$ ‰ VPDB		$\delta^{15}\text{N}$ ‰ AIR	
	Mean	St dev.	Mean	St dev.
All ( $N=18$ )	–20.2	0.37	10.7	1.12
Teeth ( $N=14$ )	–20.1	0.34	11.0	1.02
LN-EBA teeth ( $N=13$ )	–20.2	0.36	11.0	1.05
LN-EBA teeth, without outliers (MM12 and 7, $N=11$ )	–20.2	0.31	10.6	0.55
LN-EBA bone ( $N=4$ )	–20.6	0.30	9.5	0.57

in the  $\delta^{15}\text{N}$  values if the outliers (MM12 and MM7) are included or not.

The samples from skull and mandibular bones exhibit lower  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values than the tooth samples and there was a significant difference in  $\delta^{15}\text{N}$  values between bone and tooth samples (Mann–Whitney  $U$  test,  $p=0.006$ ). One of the first molars from individual MM12 (an LNII/EBA adult female with Sr isotope ratios non-local to VG) and one of the first premolars of MM7 (an EBA adult male with Sr isotope ratios non-local to VG) displayed rather high  $\delta^{15}\text{N}$  values, which at least in the first case (MM12) might indicate a breastfeeding effect. In MM7, but also in MM12, an intake of marine protein in early life is possible since  $\delta^{13}\text{C}$  is also somewhat elevated. The lowest  $\delta^{13}\text{C}$  value belongs to a mandible from a LNII juvenile (MM9), whose first molar displayed Sr isotope ratios non-local to VG (Fig. 15, SI 1).

There are too few samples and too short a time span for discussing any chronological changes. Nevertheless, some tendencies and figures of the stable isotope values over time are presented in SI 2.

The uneven numbers of samples from the three sites make it problematic to compare the stable isotope values between graves. Nevertheless, it can be noted that the  $\delta^{15}\text{N}$  values in the few samples from Österplana 27 and Medelplana 18 are slightly lower than the values measured in the human remains from Medelplana 54 (SI 2).

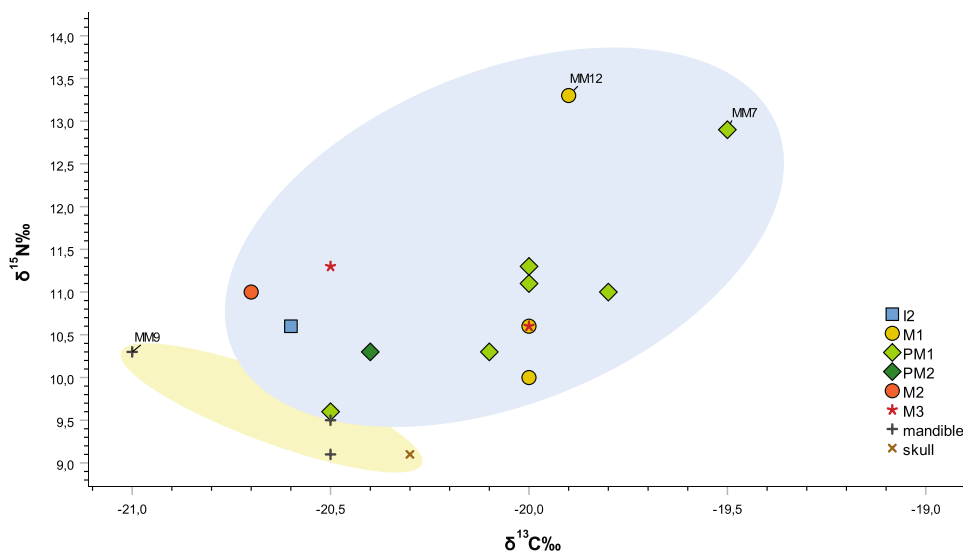
In Fig. 16, the sex and the age that the bones and teeth represent (considering the type of tooth or bone along with the estimated age of death) are presented. No distinct differences between the stable isotopes of males and females or age categories can be found (Fig. 16). Nevertheless, only males exhibit nitrogen values below 9.6‰. The groups of males with these low values are of different ages and the samples consist of four bones and a first premolar from the EBA male MM4.

### The $\delta^{13}\text{C}$ values in enamel and collagen-apatite spacing

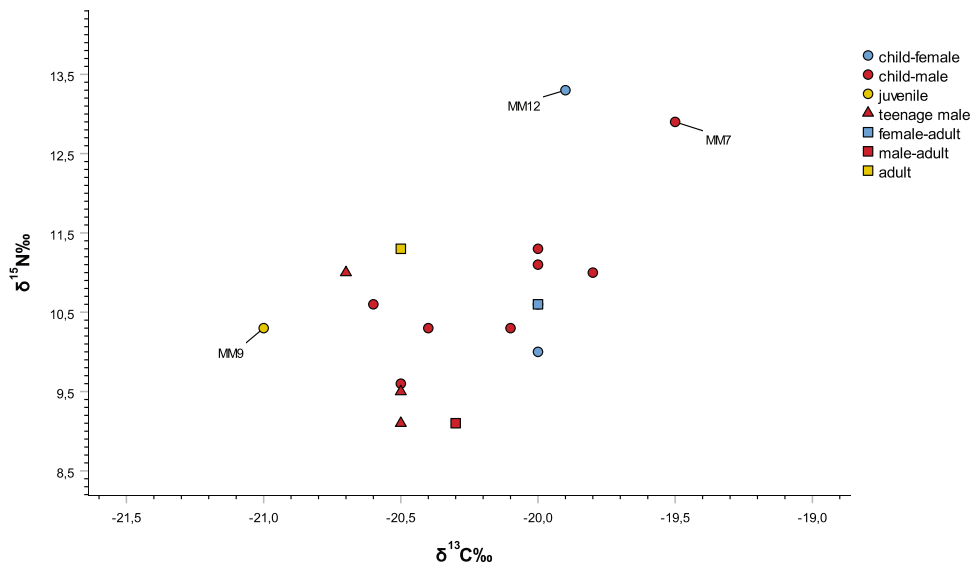
The 29 enamel samples that yielded  $\delta^{13}\text{C}$  values displayed values between –15.3 and –12.8‰ with a mean value of –14.28‰ (SI 1, Table 6). First, second, and third molars, which mirror different age spans (see “Sampling strategy and selection criteria”), were sampled. The highest  $\delta^{13}\text{C}$  values are found in the second molars (ca. 3–8 years), while the first molars (ca. 0–3 years) yielded the lowest values (Fig. 17). A statistically significant difference only occurs between these two tooth types (Mann–Whitney  $U$ ,  $p=0.020$ ). This pattern can be observed also between teeth from the same individual where the values differ up to 0.7‰ (Fig. 17). Such a difference might suggest a change in diet at, or prior to, the time of development of the enamel in the second molars.

The mean values of both  $\delta^{13}\text{C}$  in enamel and the collagen apatite-spacing only change insignificantly when the EN/

**Fig. 15** Scatterplot of  $\delta^{15}\text{N}$  (AIR) and  $\delta^{13}\text{C}$  (VPDB) values of collagen in different types of teeth and bone sampled from the 18 individuals. I, incisor; PM, premolar; M, molar. The yellow ellipse comprises the bone collagen samples, and the blue ellipse encircles the tooth dentine samples



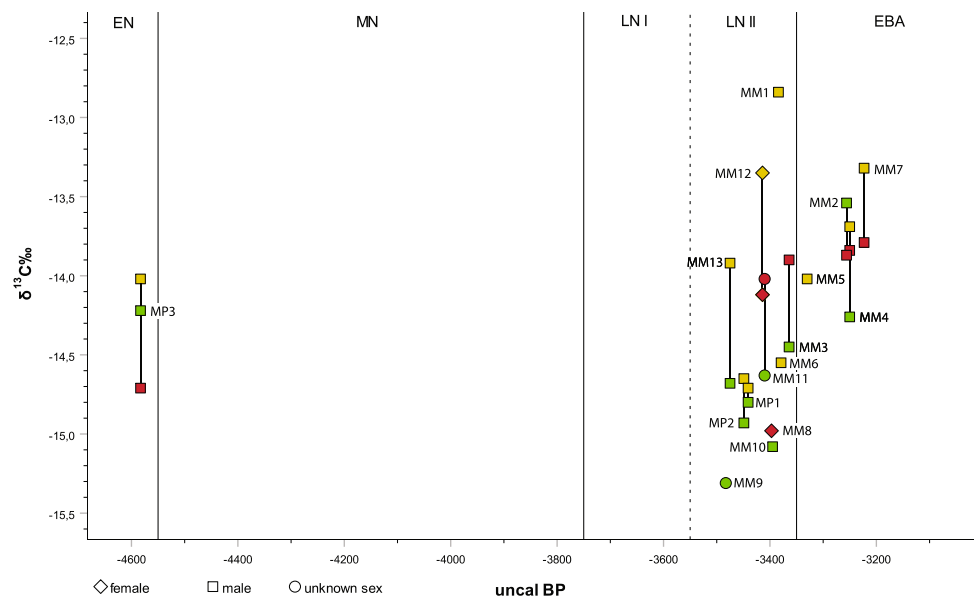
**Fig. 16** Stable isotope values of all samples grouped by biological sex and representative age group. Child, under ca. 12 years; juvenile, under ca. 20 years; teenager, ca. 12–20; adult, over 20 years



**Table 6** Minimum, maximum, mean values, and standard deviations of  $\delta^{13}\text{C}$  in enamel and collagen-apatite spacing

	$\delta^{13}\text{C} \text{ ‰ enamel}$				Collagen-apatite spacing ‰			
	Min.	Max.	Mean	St dev.	Min.	Max.	Mean	St dev.
All ( $N=29^1, 16^2$ )	-15.31	-12.84	-14.22 <sup>1</sup>	0.58	5.02	7.16	5.94 <sup>2</sup>	0.60
LN-EBA ( $N=26^1, 15^2$ )	-15.31	-12.84	-14.21 <sup>1</sup>	0.61	5.02	7.16	5.95 <sup>2</sup>	0.61
Medelplana 54 ( $N=22^1, 13^2$ )	-15.31	-12.84	-14.10 <sup>1</sup>	0.61	5.02	7.16	6.02 <sup>2</sup>	0.63
Österplana 27 ( $N=7^1, 3^2$ )	-14.93	-14.02	-14.58 <sup>1</sup>	0.33	5.17	5.79	5.58 <sup>2</sup>	0.36

**Fig. 17** A scatterplot of  $\delta^{13}\text{C}$  (VPDB) values in enamel of teeth and radiocarbon dates grouped by sex. The lines link the samples from the same individuals. Tooth types are indicated by colour. Green, first molars; yellow, second molars; and red, third molars. EN, Early Neolithic; MN, Middle Neolithic; LN, Late Neolithic; NL, non-local; VG, Västergötland



MN samples are excluded (Table 6). The collagen-apatite spacing supports an omnivorous diet with a relatively high intake of plant food (see method).

According to Fig. 17, some chronological variation of the  $\delta^{13}\text{C}$  values occurs. The lowest values can be observed in the individuals dated to the LNII, with higher values in the EBA, and the most varied values seems to appear in the transition between the LN and EBA (Fig. 17). In the periods with more than five samples (LNII/EBA and EBA), there is a significant difference between the  $\delta^{13}\text{C}$  values (Mann–Whitney *U* test,  $p=0.010$ ).

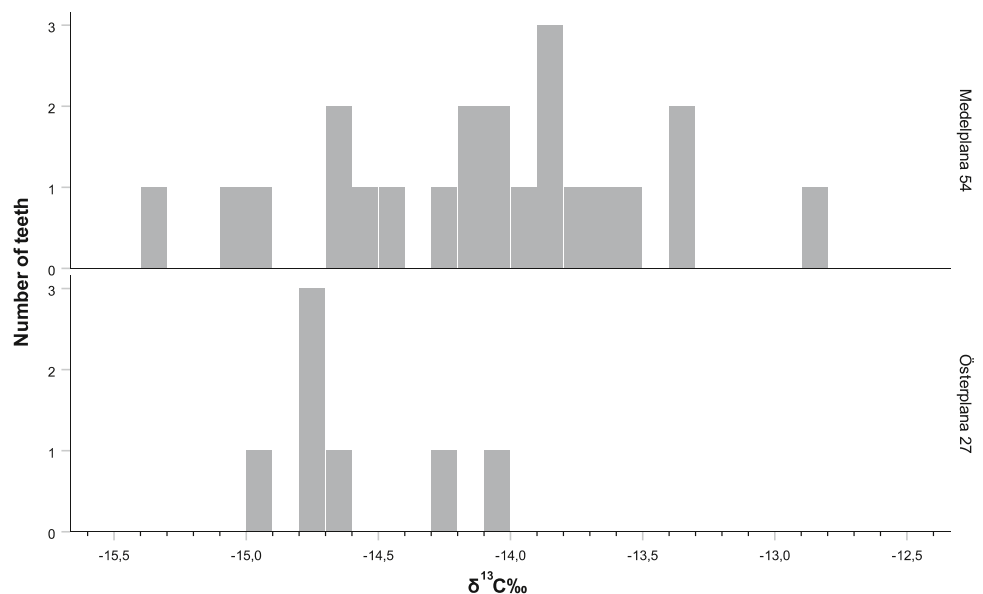
Only one female (three teeth) was identified among the individuals sampled for  $\delta^{13}\text{C}$  in enamel, while 12 of the individuals (22 teeth) could be determined as males. No

differences in the enamel  $\delta^{13}\text{C}$  values between the sexes could be observed (Fig. 17).

The values vary the most in Medelplana 54, where most of the samples derive from (Fig. 18). The Österplana 27 individuals exhibit stable isotope values in the lower part of the total range and according to the Mann–Whitney *U* test, the difference in  $\delta^{13}\text{C}$  values between the two sites is statistically significant ( $p=0.032$ ).

Collagen-apatite spacing of 16 individuals ranged between 5.0 and 7.2‰ (Table 6; Fig. S9). Most samples display collagen apatite spacings below 6.5‰. However, samples from two individuals (MM1 and MM2) buried in Medelplana 54 exhibit collagen-apatite spacings above 7‰ (Fig. S9).

**Fig. 18** Histogram of  $\delta^{13}\text{C}$  values (enamel) ‰ of teeth from Medelplana 54 ( $N=22$ ) and Österplana 27 ( $N=7$ )



## Discussion

### Burial sequences

To evaluate the time of use of the graves, we consider both the radiocarbon dates of the human remains and the typological dates of the artefacts found in the graves. It is important to point out that we are investigating the burial sequences and not the actual building of the graves. To date, the time of construction would require datable material within the grave structure (Dehn and Illum Hansen 2006).

Most of the artefacts found in the Kinnekulle gallery graves point to a use time concentrated to the last part of the LN and the first part of the EBA. This is indicated by daggers of late types, the presence of slate pendants and flint sickles, and the absence of amber beads (Anderbjörk 1932; Blank 2022). However, in two of the graves, arrowheads normally dated to the later part of the MN were recovered. These might have ended up in the grave at a later stage and might represent reused tools or possibly indicate that the typological chronologies should not always be considered absolute. Nevertheless, MN artefacts have been recovered in several graves defined as LN gallery graves in western Sweden (Blank et al. 2020).

The radiocarbon dates indicate that the three gallery graves were used contemporaneously in the LNII and EBA, although Medelplana 54 was used longer, into EB period II. The longer estimated use time probably results from the higher proportion of dated burials from this grave. The gallery graves at Kinnekulle appear in the LN II, which is a period where new house types, increased importance of metal and cultivation can be observed (Apel 2001; Artursson 2009; Vandkilde 1996). In Falbygden, the LN II is characterized by increased human mobility possibly of groups/families moving into the area (Blank et al. 2021).

Compared to Falbygden, where many of the human remains from gallery graves have been radiocarbon dated, the Kinnekulle graves seem to be slightly younger. In Falbygden, earlier LN burials have been confirmed indicating that these kinds of graves were introduced earlier in this area than at Kinnekulle (Fig. 19, Blank et al. 2020). Nevertheless, the Kinnekulle dates agree with the dating of most burials in gallery graves with port-holes in Västergötland (Blank et al. 2020).

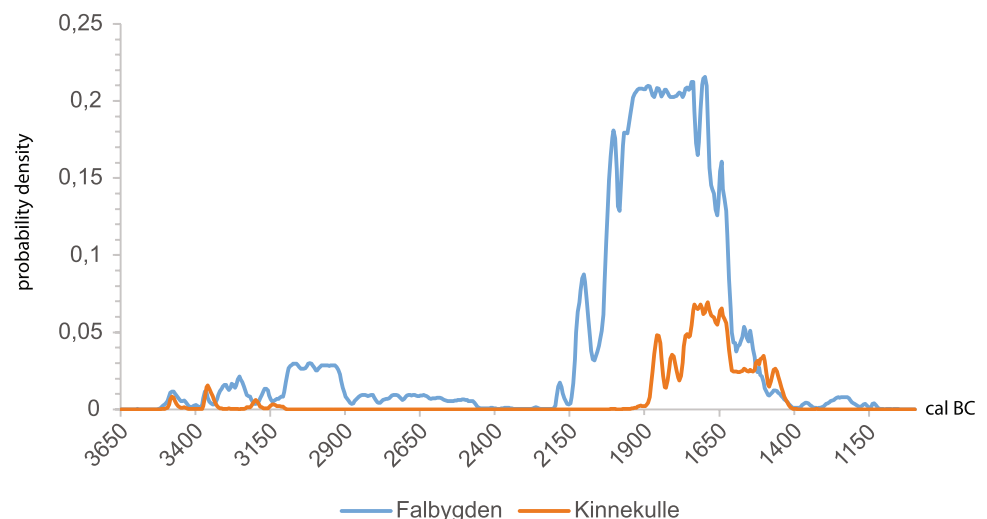
One mandible in Österplana 27 was dated much earlier, to the transition between the EN and MN periods. In Falbygden, a number of similar cases have been noted (Blank et al. 2020). There are several plausible explanations for the early find in Österplana 27. The grave might have been constructed already at this time and the bone may have been left from the first burial phase in the grave. Indications of cleaning out earlier skeletons from megalithic graves occur both during the MN and LN in Sweden (see Blank et al. 2020 for more details). A recent study of megalithic graves in the Iberian Peninsula (Aranda Jiménez et al. 2020) suggested that cleaning out bones has resulted in earlier dates of teeth than of bone which represent the latest burial phase in the grave. The mandible might also have been put in the grave during the LN and may be a relic of an ancestor deposited in the new grave (see Blank et al. 2020 for further discussion).

To sum up, the gallery graves at Kinnekulle were used for up to 300–400 years in the LNII to the EBA period I/II. Considering the MN artefacts and the EN/MN human bone, a previous burial sequence in the graves during the MN may be possible, although these items may as well have been deposited in the graves during the LN.

### Health and trauma

The observed caries frequency of 6.9% is comparable to other contemporaneous localities in southern Sweden (Blank et al.

**Fig. 19** Radiocarbon dates of buried individuals in gallery graves in southwestern Sweden. Falbygden  $N=104$ , Kinnekulle  $N=18$ , data from Blank et al. (2020)



2018a; Tornberg 2013, 2016). Evidence of linear enamel hypoplasia (11.3%) is also in line with the contemporaneous and geographically close locality of Falköping stad 5 (Blank et al. 2018a), while cribra orbitalia (25%) is significantly more common than in the Falköping stad 5 and the Scanian Abbekås materials (Blank et al. 2018a; Tornberg 2013), but similar to, or less common, than what is reported in other contemporaneous European skeletal assemblages (e.g. Bennike 1985; Wittwer-Backofen and Tomo 2008). It seems that people in Neolithic-BA Scandinavia generally show fewer signs of pathologies related to diets rich in carbohydrates as well as less evidence of nutritional stress than populations in more southern latitudes (e.g. Cunha et al. 2007; Wittwer-Backofen and Tomo 2008). The reason is difficult to assess, but probably foods rich in sugars, such as berries, fruits, and honey, were likely not as common in the diet in the north. Furthermore, signs of malnutrition are often caused by illness in the childhood, such as infections. As endemic infections are more likely to spread and sustain in more densely populated areas (Cockburn 1977: 109), the risk of large outbreaks of infectious disease was probably limited in the Kinnekulle area where population density presumably was low.

There is a general scarcity of remains from subadult individuals in the Kinnekulle gallery graves, especially regarding the youngest age groups. It is possible that the low frequency reflects a real decreased childhood mortality related to a generally low population density, thus, with a low risk of infectious disease mortality (Ahlström 2015), but could, in accordance with the osteological paradox (Wood et al. 1992), be reflective of low fertility. Generally, the number of child deaths is more related to fertility than it is to mortality, since a relatively large proportion of children are expected to die in the first years of life due to frailty to infections (ibid). However, other reasons such as high levels of taphonomic loss, recovery bias, but also burial practices (see section below) might also explain the few remains of subadults.

Viewing the Kinnekulle remains in relation to the geographically close Falbygden, the proportion of subadults is substantially lower (Blank 2021; Tornberg 2018), which might be related to a significantly less dense population in the Kinnekulle area. In fact, the proportion of subadult remains from Falköping stad 5 is higher than from contemporaneous sites in Scania (Blank et al. 2018a; Tornberg 2018), possibly reflecting a general correspondence between the number of gallery graves and population density (stationary or related to ritual/social gatherings) in this small geographical region. Better preservation for bones in the Falbygden area is also a plausible contributor to the pattern.

Both Medelplana 54 and Österplana 27 exhibit evidence of violence. Two individuals in each grave show signs of skull trauma. Although skull trauma might be caused by accidents, the placement and morphology of the injury in these cases rather reflect intentional violence. Depressed

fractures above the hat brim line are more commonly found in cases of intentionally induced skull trauma, while linear fractures in the lower part of the back of the head more often is associated with falls (Ehrlich and Maxeiner 2002; Kremer et al. 2008; Li et al. 2021; Lovell 1997; Symes et al. 2012; Walker 1989). There seems to be no difference in the frequency of violence-related skull trauma between the Kinnekulle area and contemporaneous assemblages from Falbygden and Scania. In Falbygden, all of the skull trauma found in megalithic graves can be dated to the LN, which might indicate increased levels of violence from the MN to the LN in this area (Blank 2021: 111-112). This might be related to a probable population increase in the LN in general, where social stratification may have been more evident. Between 8.5 and 13% of the adult individuals inhumed in gallery graves in Västergötland and Scania had suffered from violence related skull trauma, both healed and unhealed (Tornberg 2022). There is, however, a tendency towards higher levels of skull trauma in individuals inhumed in gallery graves than in other types of burials from the same period. Flat graves exhibit the lowest frequency (3.6%) and EBA barrows exhibit intermediate levels (11.1%) (Tornberg 2022). Most of the gallery grave remains are from the Västergötland region, while the analysed remains from flat graves and barrows are of Scanian origin (Ibid.). It is possible that the difference in frequency reflects regional differences in the presence of violence, but aspects like chronological differences and/or social differences between inhumations in the different burial types, hence different risk of violence, are other possible interpretations. It is, however, evident that violence (and warfare?) occurred regularly in LN-EBA southern Sweden, with frequencies of skull trauma exceeding, e.g. that of the famous Middle Bronze Age battlefield of Tollense. Here, 7% of the victims evidenced ante- or peri-mortem skull trauma (Brinker et al. 2016), almost half of what is evident in south Swedish gallery graves. This difference might, however, be related to battle tactics, weaponry, and general differences in the use of violence.

### Kinship and megalithic graves

Burying only 1.7 to 5 individuals per generation (see “Result”) is a low number compared to what can be expected from a group. One explanation could be that most of the people were interred in other types of graves and only a selected few were placed in gallery graves. Another possibility is that the graves were cleared out of old skeletal remains (see above). A further probable reason for the few burials compared with the long use time might be that the graves were intensively used for a few shorter periods of a few years spread over several hundreds of years.

It has been proposed that the interred in Funnel Beaker megaliths may represent a segment of the population, such

as a certain hierarchical level of society, and/or certain families or groups (Blank 2021; Sjögren 2003). The LN gallery graves have been suggested to be graves reserved for a ruling elite (Artursson 2009). Others (Holm et al. 1997; Weiler 1994) regard gallery graves as family graves for the local population. Certain individuals or families from a larger geographical area may have buried their dead in the gallery graves of Kinnekulle, which may explain some of the non-local Sr isotope ratios measured in human teeth recovered from the graves.

Close kinship relations have been proven in Neolithic megalithic graves in England, Ireland, and Sweden (e.g. Cassidy et al. 2020; Fowler et al. 2022; Sánchez-Quinto et al. 2019) with the help of aDNA. Differences in the frequencies of mtDNA haplogroups between gallery graves have been noted in Falbygden, which may result from restricted mating patterns, and in some cases, a haplogroup was shared among several individuals, which may indicate maternal kinship relations within graves (Blank et al. 2021). The eight Kinnekulle individuals that yielded mtDNA data all displayed unique haplotypes, which excludes close maternal kin relations, at least between these eight individuals (SI 1). We can, however, not exclude possible kinship relations among individuals at Kinnekulle, until autosomal DNA data from more individuals are analysed. The occurrence of extra sutural bones/ossicles in eight out of twenty individuals in Österplana 27 may, for example, result from genetic affinity (see “Osteology and genetic assessments”).

An equal number of males and females of different ages were buried in these graves, but as already discussed, subadults are few. Young children may not have been considered fully integrated in the community, and therefore not treated in the same way in burial rituals (Hertz 1960: 76). For example, infants have, in some cases, been found buried in settlement contexts (post-holes of houses and below house floors etc.) and not in regular graves (Conklin and Morgan 1996: 672; Hutton 1927; Ucko 1969: 270-271). Thus, the lack of remains from subadults in the gallery graves at Kinnekulle may reflect differences in burial practices of age groups as well as differences in child mortality rates and population density between Kinnekulle and Falbygden. Most probably, only part of the population was placed in the gallery graves at Kinnekulle, maybe groups (family or kin-related) of a certain status.

### Mobility and exchange networks

According to the Sr isotope ratios of teeth from the individuals buried in the Kinnekulle gallery graves, only two individuals exhibited local ratios to Kinnekulle in all their sampled teeth, while four displayed non-local ratios to Kinnekulle but local to Västergötland, and another eleven individuals yielded ratios non-local to Västergötland.

Of the ratios non-local to Västergötland, one individual exhibited low values, which are found at the Swedish west-coast, in parts of Scania, at Öland, in Denmark, and in coastal Estonia, etc. (Arcini et al. 2016; Bergerbrant et al. 2017; Fornander et al. 2015; Fraser 2018: 61; Frei and Frei 2011; Frei and Price 2012; Klassen et al. 2020; Oras et al. 2016; Sjögren et al. 2009; Wilhelmson and Ahlström 2015). The Swedish west-coast, Scania, and/or Denmark are the most plausible origins considering the provenience of most of the flint finds in the graves (see below). The remaining ten individuals display high Sr isotope ratios which have been found in more eastern and northeastern regions with older bedrock (Åberg 1995; Åberg and Wickman 1987; Löfven-dahl et al. 1990; Price et al. 2021). Two of the individuals, a male and a female, displayed Sr isotope ratios above 0.733 (MM7 and MM12). They also displayed the highest  $\delta^{15}\text{N}$  values measured in the dentine samples.

Considering the different molars sampled from the individuals, movements between locations in the Precambrian terrains and Kinnekulle were indicated. Furthermore, Sr isotope ratios in the different molars of the EN/MN individual MP3 indicate that this individual spent his early childhood in areas with low ratios, such as the Swedish west-coast, Scania, or Denmark and moved to the Precambrian regions of southwestern Sweden in late childhood/youth. This mandible may be the remains of an individual, originating from one of the regions suggested above, buried at Kinnekulle in the transition between the EN and MN periods. In another adult male, MM4, the Sr isotope ratios support a move to Kinnekulle at the age of 3 to 8 years from the surrounding Precambrian area.

Only three individuals exhibited Sr isotope ratios falling in the Kinnekulle local range in at least one tooth, suggesting that the rest, 17/20 (85%), moved into the area in their adult lives or spent their whole lives outside of Kinnekulle and were only brought there to be buried. The observations might suggest that mostly adults moved in from different locations in the Precambrian areas and were buried in gallery graves. Considering the small size of the mountain plateau, it seems possible that agricultural lands may have been located on different geological units with different biologically available Sr on the plateau but also beyond, and resources from the surroundings may also have been used. Such landuse patterns may have contributed to the observed variation among different individuals and among teeth from the same individual.

It is also important to point out that no less than 11 individuals yielded Sr isotope ratios that indicate that they spent their childhood even further away from Kinnekulle, outside of Västergötland. A high degree of mobility, including long distance movement, in inland southwestern Sweden in the LN-EBA has been proposed based on Sr isotope data from Falbygden (Blank et al. 2021). As in Falbygden, the highest

variability in Sr isotope ratios occur in the LNII-LNII/EBA (Ibid.).

Many of the mtDNA haplogroups found in this study are known from other Neolithic contexts in Scandinavia and northern Europe (Allentoft et al. 2022; Bergerbrant et al. 2017; Fraser et al. 2018a, b; Günther et al. 2018; Malmström et al. 2009, 2015, 2019; Skoglund et al. 2012, 2014).

In general, the mtDNA haplogroups of the LN and EBA individuals in the gallery graves at Kinnekulle concur with the haplogroups found in MN and LN/EBA skeletal remains from megalithic graves in Falbygden (Allentoft et al. 2022; Blank et al. 2021). Interestingly, the MN haplogroups in Falbygden, which seem to have disappeared in the LN, were absent also in the LN/EBA remains from Kinnekulle. For example, the I4 group, which is first seen at Kinnekulle in the EBA, is a new group that appears during the LNII in Falbygden. The T2 and U4, also present in the Kinnekulle samples, are two of the other groups that are first seen in the LN/EBA in the skeletal remains from Falbygden (Blank et al. 2021). This implies that new genetic populations were moving into the region during this time. This is especially interesting when adding the Sr isotope data indicating a high proportion of non-locals.

Considering the distribution of LN and EBA stray finds at Kinnekulle and the neighbouring areas (Blomqvist/Bägerfeldt 1990; Weiler 1994), it seems likely that most of the buried individuals lived most of their lives outside of Kinnekulle and were only buried there. The variation in stable and Sr isotopes between the different graves may also indicate that the graves were used by different (kinship-) groups with different residential origin and/or various networks. The Kinnekulle mountain might have been reserved for burials and linked to ancestors. The accessibility of limestone is also a reason for building the megalithic graves at Kinnekulle. It is also possible that the area was an important gathering place for people living in the surrounding regions as suggested by the large rock art panels. More knowledge about possible settlements in the nearby area is needed.

The inland of southwestern Sweden during the LN end EBA is often perceived as peripheral to Scania and Denmark (Apel 2001; Kristiansen & Larsen 2005; Skoglund 2009). The only available flint at Kinnekulle is Cambrian flint, which was recovered from the Medelplana 54 grave. The local Cambrian flint has been found in LN gallery graves for example in Rångedala in southern Västergötland, indicating regional networks. The remaining flint deposited in the graves was of south Scandinavian type and most probably originated from Scania or Denmark. Thus, both the MN and LN-EBA flint artefacts show the presence of networks (direct or indirect) with Scania and/or Denmark. Most of the LN daggers recovered in the graves display a high degree of technical skill, such as parallel flaking and punched seams. According to Apel (2001), these kinds of knapping

techniques indicate that the daggers were imported from Denmark or southern Scania. However, skilfully pressure flaked arrowheads made in Cambrian flint indicate that at least some of the arrowheads were locally produced. The Sr isotope samples from the EN/MN individual indicate direct movement from the more southern regions at this time, while no such relation was observed in the later Sr isotope samples. However, short-term movements are difficult to trace using Sr isotope analysis.

Apart from pendants, slate artefacts are uncommon in Västergötland during the LN-EBA. Slate pendants are common in graves dated to the LN and EBA in Scandinavia with the highest frequency in Sweden. Sources of good quality slate are present in western Sweden, for example west of lake Vänern in Dalsland and in the more eastern region of Närke (Taffinder 1998). In both these areas, gallery graves with port-holes occur. Thus, the slate may be from a regional source, although the manufacturing and use of pendants reveal a more widespread shared ideology.

No bronze, gold, or amber accessories or jewelry, which appear in several gallery graves in southwestern Sweden were found in the Kinnekulle graves (Weiler 1994). The lack of amber artefacts might reflect poor preservation conditions or that these objects often appear in early LN contexts (Anderbjörk 1932; Blank 2022), while the absence of metal objects may result from looting. Another explanation may be that import objects in general were less accessible in this area.

The presence of late dagger types and the late burials along with the lack of metal and amber might suggest that groups in the surrounding areas of Kinnekulle engaged in indirect long-distance networks at a later stage of the LN than other areas such as central Västergötland and Falbygden. Thus, the Kinnekulle area would have been even more peripheral to the southern regions of Scandinavia than Falbygden and many other locations in Västergötland considering the long trade metal and flint networks existing in LN-EBA Scandinavia (Vandkilde 1996). The large proportion of human remains with high Sr isotope ratios might indicate that networks extending to more eastern and northeastern directions may have been dominant here during the LN-EBA. Furthermore, the large rock carving site with several parallels to the west coast (Weiler 1994: 92), in the southeastern fringe of Kinnekulle dating back to the EBA, suggest that the area was an important regional node at that time.

## Diet and subsistence

The stable isotope data indicate a terrestrial omnivore diet with a relatively high intake of plant foods. The significant difference observed in  $\delta^{15}\text{N}$  values between the tooth and bone samples probably reflects a shift between childhood



and adult diet, with protein intake from lower trophic levels in adults. Furthermore, comparisons of the stable isotope data among sites revealed higher  $\delta^{15}\text{N}$  collagen and  $\delta^{13}\text{C}$  enamel values in Medelplana 54. Differences between sites considering stable isotopes have been observed in previous studies of both MN and LN-EBA individuals in Falbygden (Blank 2021; Sjögren 2003). These differences may have resulted from slight variations in consumption patterns and/or subsistence strategies between nearby sites. However, mobility patterns, for example people originating from different places at the various sites, may also be reflected in the stable isotope signals that go back to the childhood. The individuals (MM12 and MM7) with the highest non-local Sr isotope childhood ratios also displayed the highest  $\delta^{15}\text{N}$  values. Furthermore, a shift of  $\delta^{13}\text{C}$  enamel values as well as strontium isotope ratios between the first and second molar was observed in MM4. There is also a statistically significant difference of collagen-apatite spacing between the two non-local groups, within Västergötland and outside Västergötland (SI 2), suggesting over-regional differences.

The Kinnekulle samples displayed slightly lower collagen apatite spacing and higher  $\delta^{15}\text{N}$  values than the LN-EBA megalithic population of Falbygden (Blank 2019, 2021; Fig. S7, S8). A plausible explanation is that the Kinnekulle individuals had higher proportions of fish and domestic animal-based foods in their diets than the people buried in the Falbygden megalithic graves. Noteworthy is, that the MN and the LN-EBA individuals of Falbygden, a diet more reliant on plant foods than in more eastern regions of Sweden has been proposed based on stable isotope data (Blank 2021). Furthermore, the proximity to lake Vänern may also have resulted in a heavier reliance on freshwater fish of the people from Kinnekulle compared to the ones in Falbygden, although  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values do not suggest more than marginal consumption of protein from freshwater sources.

In the LN period, increasing farmland, pastures, and forest clearance is indicated in the pollen data of the region (Berglund 2003; Enevold 2019; Fries 1951, 1958). The appearance of new find categories such as shaft-hole axes and flint sickles in large numbers and in new areas also suggests expanded cultivation. In the investigated gallery graves, one sickle was recovered, which indicates the presence of cultivation. At Kinnekulle, only a few scattered shaft-hole axes have been found, although high concentrations occur in the Precambrian area south and southwest of Kinnekulle (Blomqvist/Bägerfeldt 1990: 26, Weiler 1994: 113). This may indicate that most of the cultivation activity took place outside of Kinnekulle. Macrofossils and pollen analyses would be needed to further investigate this.

In two of the graves, scrapers were found, which may be associated to hide and skin preparation. Thus, keeping of livestock and/or hunting were probably part of the subsistence strategies and there were many uses of the animals. The

arrowheads recovered in the grave may have been related to hunting, although they are mainly interpreted as part of the weaponry of the “male warrior” along with the daggers (Apel 2001; Vandkilde 1996).

Subsistence economy with cultivation and husbandry is suggested and a terrestrial diet with a substantial intake of plant foods as implied by the collagen-apatite spacing and some consumption of freshwater fish. The high variability in  $\delta^{15}\text{N}$  values could indicate varied agro-pastoral strategies or/and high human mobility. Considering the Sr isotope as well as the stable isotope data, most of the individuals may have been living in agriculture-based groups in nearby locations outside of Kinnekulle, at least seasonally.

## Conclusion

The numerous gallery graves found at Kinnekulle reveal that the area was an important place for burial rituals, probably also for the commemoration of ancestors. Radiocarbon dates of human remains and finds from three of these graves indicate a use time spanning from the LNII, a time of substantial transformations, into the BA period II. There are no known graves from earlier periods, although one human bone from Österplana 27 was dated to the EN/MN period. The Sr isotope values of this individual are in accordance with the Sr signals found at the Swedish west coast, Scania, and Denmark.

The mtDNA haplogroups found in the Kinnekulle gallery graves agrees with mtDNA data from human remains dated to the same period from megalithic graves in Falbygden. The data support new groups appearing in southwestern Sweden during the LN that were not present in the MN period.

The Sr isotopes from the buried LN-EBA individuals indicate that most of them spent their childhood outside of the sedimentary area of Kinnekulle. The Sr isotope data and the distribution of stray finds and rock art sites suggest that the mountain plateau of Kinnekulle was reserved for the dead, while the people lived in the surrounding lower lying regions.

The stable isotope data and the archaeological circumstances indicate a subsistence economy based on cultivation and husbandry with a terrestrial diet and a substantial intake of plant foods. The relatively high  $\delta^{15}\text{N}$  values, compared to other contemporary inland human remains, suggest that fishing also was part of the economy, although marginal, which seems logical considering the vicinity to the large lake Vänern.

The skeletal remains from the Kinnekulle area provide evidence of pathological lesions associated with general physiological stress and trauma comparable to other contemporaneous assemblages from Falbygden and Scania. The level of dental caries is similar to other contemporaneous

sites. It is evident that some of the individuals suffered from violence, but the levels of violence related trauma are not different from what is present in other LN-EBA gallery graves. Although many similarities could be observed between Kinnekulle and other regions, the late dates of the Kinnekulle remains and artefacts support the view of the area as a peripheral part of the Scandinavian Late Neolithic cultural expression.

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**Author contribution** Malou Blank and Anna Tornberg conceived the study. Conceptualization, visualization, material preparation, and data collection were performed by Malou Blank and Anna Tornberg. Malou Blank prepared all figures and tables. Osteological analysis was conducted by Anna Tornberg and archaeological and isotopic data analyses were performed by Malou Blank. Sampling for biochemical analyses was done by Anna Tornberg, Jan Storå, and Malou Blank. Helena Malmström, Magdalena Fraser, Corina Knipper, and Karin M Frei performed laboratory work, data analysis, and data curation. Malou Blank and Anna Tornberg wrote the original draft and finalized the manuscript with input from all other co-authors.

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**Data availability** All relevant data are within the paper and its supplementary information files.

**Code availability** Not applicable.

## Declarations

**Ethical approval** The study and paper follow ethical standards. Ethical statements are not relevant to this study.

**Consent to participate** All authors approved to participate in this paper.

**Consent for publication** All authors approved to publish the results of this study.

**Competing interests** The authors declare no competing interests.

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