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# The "post-weanling's conundrum": exploring the impact of infant and child feeding practices on early mortality in the Bronze Age burial cave of Moro de Alins, north-eastern Iberia, through stable isotope analysis

Teresa Fernández-Crespo[1,2] · Rick J. Schulting[1] · Andrea Czermak[1] · Javier Ordoño[3] · José Ignacio Lorenzo[4] · José María Rodanés[5]

## Abstract

The relationship between infant and child feeding practices and early mortality is difficult to address in past societies. Here, stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope measurements of bulk bone and sequential dentine samples of deciduous second and/or permanent first molars of four younger children, one older child, one late adolescent, and two young adults ($n = 8$) from Moro de Alins cave, north-eastern Iberia, are used to explore the potential impact of early-life nutrition on mortality in the Bronze Age. Isotope results are compatible with generally short exclusive breastfeeding and standard weaning periods compared to other pre-modern populations. However, there are differences in exclusive breastfeeding mean $\delta^{13}C$ values and in $\Delta^{13}C$ trophic shifts between exclusive breastfeeding and immediate post-weaning isotope values for those individuals who survived into adolescence and adulthood and those who did not. While the former seem to be consistent with trophic distances published for modern mother–infant pairs, the latter are above most of them. This may suggest that individuals who consumed similar foods to their mothers or suffered from less physiological stress during or after weaning had greater chances of survival during early childhood and beyond. Post-weaning seems to have been a particularly stressful period of life, where a number of instances of patterns of opposing isotopic covariance compatible with catabolic changes, often preceding death among non-survivors, are detected. This outcome shows the key role of nutritional and/or physiological status in early-life morbidity and mortality among partially and especially fully weaned children from pre-antibiotic, pre-vaccination, and poor sanitation contexts and proposes that adult survival is rooted in early life experiences, in keeping with the developmental origins of health and disease.

**Keywords** Stable carbon and nitrogen isotopes · Breastfeeding and weaning practices · Survival · Life history theory · Late prehistory · Spain

✉ Teresa Fernández-Crespo
teresa.fernandezcrespo@uva.es

[1] School of Archaeology, University of Oxford, Oxford, UK

[2] Departamento de Prehistoria, Arqueología, Antropología Social y Ciencias y Técnicas Historiográficas, Universidad de Valladolid, Valladolid, Spain

[3] Departamento de Arqueología y Nuevas Tecnologías, Arkikus, Vitoria-Gasteiz, Spain

[4] Decanato, Colegio Oficial de Doctores y Licenciados en Filosofía y Letras y Ciencias de Aragón, Zaragoza, Spain

[5] Departamento de Ciencias de la Antigüedad, Universidad de Zaragoza, Zaragoza, Spain

## Introduction

Breastfeeding is known to be a powerful mediator of infant health and survival. As generally the sole source of nutrition in the first 6 months of life, breast milk plays a critical role in optimal growth and development. It provides all nutritional needs during infancy, as well as important immunomodulatory and anti-inflammatory factors that help augment and regulate immature immune systems (Lönnerdal 2000). Around 6 months of age, however, nutritional needs start to exceed what is provided by breastmilk, and complementary foods (i.e., nutritive solids or liquids consumed alongside breastfeeding) become necessary to fill the energy

and nutrient gaps (Kramer and Kakuma 2004). In most traditional societies, weaning ends around 2.5 to 3 years of age (Jay 2009), although variation from less than 1 to over 5 years of age has been found (e.g., Fulminante 2015).

Suboptimal feeding practices, particularly the early introduction of complementary foods (i.e., prior to 6 months) and the early cessation of breastfeeding (i.e., complete weaning before 2 years of age), especially in contexts where sanitation is poor or environmental pressures exist, have been regularly associated with elevated risks of infant morbidity and mortality (Black et al. 2008). Exposure to environmental pathogens through the new foods and/or a poor diet is often linked to intestinal and immune dysfunctions, which particularly affect those with less mature systems (e.g., Hanson et al. 2001; Martin and Sela 2013). The "weanling's dilemma" is recognized as the health trade-off faced by an infant confronted with complementary foods potentially contaminated with pathogens against the probability of diminished growth and development when exclusive breastfeeding continues for too long (e.g., Katzenberg et al. 1996). However, the applicability of this concept has recently been called into question (Kendall et al. 2021). It has been proposed that a perceived negative association between prolonged nursing with complementary feeding and poor health and a pervasive underestimation of the protective role provided by breastmilk in the bioarchaeological literature may be behind such a concept. Nevertheless, the detrimental effects of contaminated food stuffs certainly were and remain a real danger for weaning health and survival, particularly in hostile environments (e.g., Rowland et al. 1978; Black et al. 2008). Certainly, the weaning process should not be seen as an inherent source of physiological stress, but the role of breastfeeding in ameliorating relative risk is not absolute. Some observational studies of present-day low- and middle-income countries (LMIC) have suggested similar mortality rates for weaning and weaned individuals of the same age ranges and socio-economic circumstances, except for crisis situations, such as war, where the nutritional and protective effects of breastfeeding remain essential for maintaining health (e.g., Jakobsen et al. 2003). Thus, the view of the "weanling's dilemma" as merely a "negative" perception seems unsupported.

Due to the traditional emphasis on the "weaning process" as the most perilous period of juvenility, it is less recognized that exposure to pathogens may be more harmful once weaning is complete and infants no longer benefit from the immunological buffer of breastfeeding. This situation is here referred to as the "post-weanling's conundrum." The deficiency of secretory antibodies, particularly of immunoglobulin A (IgA) whose levels are not believed to reach adult values until ca. 6 years of age (Burgio et al. 1980), seems to play a major role in the pathogenesis of respiratory and gastrointestinal infectious diseases common in infancy and early childhood, as well as in the heterogenous and usually naïve (i.e., slower and more attenuated) immune responses mounted by fully weaned individuals (Weemaes et al. 2003). Furthermore, infants and children are more likely to be malnourished and ill in the post-weaning period, especially in deprived environments, because they lack the nutritional support of breastfeeding and may rely on monotonous, plant-based diets of low nutritional quality (e.g., Filteau 2000; Solomons 2007) and because access, transport, and storage of safe drinking and cooking water is often complicated (e.g., Ball and Pickford 1982). Sufficient clean water facilitates better hygiene practices, which is a key measure to prevent not only diarrheal diseases, but also acute respiratory infections (UNICEF 2008). The synergistic relationship between infection and nutritional deficiency is the greatest cause of death in infants younger than 5 years old in present-day developing countries (e.g., Cho and Suskind 1983; Onofiok and Nnanyelugo 1988; Scrimshaw et al. 1990), and this was probably also the case in most preindustrial societies. Of course, just as with the weaning period, it should not be assumed that the post-weaning period was necessarily stressful for all individuals. Inter- and intra-population variation is to be expected, with some groups and individuals experiencing little to no physiological stress. Parental decisions on infant-rearing practices are varied and depend on several cultural, socio-economic, and environmental factors, including the cost/benefit balance of caregiving (Quinlan 2007), the intention to produce other offspring (i.e., lactation amenorrhea; Borgerhoff-Mulder 1992), and the availability of safe and nutritious foods (e.g., Almedon and De Waal 1990; Lindstrom and Berhanu 2000), whose material evidence is almost invisible in the archeological record (for an exception, see Dunne et al. 2019).

From the late 1980s, analysis of stable carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) isotopes of human tissues has proven effective in the reconstruction of breastfeeding and weaning practices in past populations (e.g., Fogel et al. 1989; Lee-Thorp 2008), because the $^{13}$C and $^{15}$N composition of body tissues (e.g., bone, tooth dentine, hair, nail) reflects the food consumed by an individual (DeNiro and Epstein 1978, 1981). Generally, $\delta^{15}$N values among exclusively breastfed infants are accepted to be elevated by ~ 2 to 3‰ above those of their mothers due to a trophic level shift, based on the isotope values of fingernails from modern mother-infant pairs (Fogel et al. 1989: ~ 2.4‰; Fuller et al. 2006: ~ 2–3‰; Herrscher et al. 2017: ~ 2–2.8‰). However, there is less agreement amongst studies about the extent of a $\delta^{13}$C trophic shift. An oft-cited study of fingernail clippings from five mothers and their exclusively breastfeeding infants suggested the $\delta^{13}$C trophic shift is ~1‰ (Fuller et al. 2006). However, an earlier study of 17 mother-infant pairs provided nearly identical values for $\delta^{13}$C (Fogel et al. 1989). Similarly, a more recent study based on a single mother-infant pair suggested a

$\delta^{13}C$ trophic shift of < 0.5‰ (Herrscher et al. 2017). In any case, isotope values will tend to decrease in both systems as complementary foods are progressively introduced (unless, of course, these differ isotopically from the mother's diet during lactation) and generally fall to a similar level as the mothers after the complete cessation of nursing (Fogel et al. 1989; Fuller et al. 2006).

In bioarchaeological research, past weaning practices have generally been investigated using bone collagen from infants and children that was forming at the time of death (e.g., Pearson et al. 2010; Richards et al. 2002; Stantis et al. 2019; Tsutaya et al. 2015), with isotopic ratios in this tissue mainly representing the "average" diet over the period of bone turnover, generally accepted to be ca. 10 years or more in adults and less in non-adults resulting from more rapid turnover during skeletal growth (e.g., Hedges et al. 2007). Infant and child bone collagen isotope ratios plotted against estimated age-at-death can provide a broad approximation of the timing and duration of exclusive breastfeeding, weaning, and the post-weaning period at a population level (Reynard and Tuross 2015). However, research has recently suggested that juvenile bone collagen may not be a reliable source for reconstructing past early lifeways (e.g., Beaumont 2020; Beaumont et al. 2018; Fernández-Crespo et al. 2018). The fractionation process through which $\delta^{13}C$ and $\delta^{15}N$ isotopes are incorporated into body tissues can be affected by in vivo metabolic activity (e.g., Minagawa and Wada 1984) resulting from malnutrition, illness, or other physiological factors (e.g., Dailey-Chwalibóg et al. 2020; Fuller et al. 2005; Neuberger et al. 2013). Although the effect of growth on stable isotope ratios is not supported by some studies (Waters-Rist and Katzenberg 2010), it seems that bone collagen, especially if growth is stunted, may fail to adequately record dietary and physiological isotope signatures (e.g., Beaumont et al. 2018). Moreover, the validity of dietary assessments using data from children who died before reaching adulthood (i.e., the "Osteological Paradox"), has been called into question (e.g., Katzenberg et al. 1996; Wood et al. 1992).

The recent development of high temporal resolution microsequential isotopic analysis of dentine (e.g., Beaumont et al. 2013; Czermak et al. 2020; Eerkens et al. 2011; Stantis et al. 2021) has permitted the reconstruction of past early life-histories with sub-annual resolution (e.g., Fernández-Crespo et al. 2020; Montgomery et al. 2013), potentially teasing apart the effects of diet and physiological stress at an individual level (e.g., Beaumont and Montgomery 2016; King et al. 2018; O'Donoghue et al. 2021). This is possible because primary dentine grows incrementally (Nanci 2008) and, in contrast to bone, does not remodel once formed. Moreover, its gross development is believed not to be affected by environmental insults, such as malnutrition or illness (e.g., Elamin and Liversidge 2013), although these are recorded at a microscopic

level (e.g., alteration in matrix secretion) (Beaumont and Montgomery 2016; Beaumont et al. 2018). Particular attention has recently been paid to isotopic patterns of opposing covariance. It is now recognized that the isotopic discrimination between the body and the diet (i.e., the trophic shift) varies between subjects according to their particular metabolic state, leading to non-concomitant changes in $\delta^{13}C$ and $\delta^{15}N$, in contrast to those typically resulting from dietary inputs. For example, catabolism of bodily protein caused by weight loss, associated with malnutrition as a result of morning sickness during pregnancy or anorexia nervosa, has been commonly associated with an increase in $\delta^{15}N$ values (e.g., Fuller et al. 2005; Mekota et al. 2006). Further, the breakdown of $^{13}C$-depleted body fat deposits to compensate for a lack of dietary carbohydrates and proteins—which are normally the carbon source for tissue synthesis— is likely to cause a decrease in $\delta^{13}C$ values, though this relationship is considerably more complex than that for nitrogen (Doi et al. 2017; Neuberger et al. 2013). Conversely, instances of the opposite trend, particularly observable as dipping $\delta^{15}N$ (and occasionally rising $\delta^{13}C$) values, have been related to anabolic change as a result of an increase in body mass associated with pregnancy (Fuller et al. 2005) and perhaps to growth spurts (Millard 2000; Tsutaya 2017).

Moro de Alins cave, located in the southern slopes of the Pyrenees, in the Huesca province of north-eastern Iberia (Rodanés 2017a), serves here as a case study for exploring Bronze Age infant and child lifeways. The presence of a number of juvenile human remains in this cave suggests high non-adult mortality (Alconchel 2017), allowing us to explore the impact of early feeding practices (such as the duration of exclusive breastfeeding, the duration and graduality of the cessation of nursing, and the type of weaning and post-weaning foods) on infant and child health and mortality.

To this end, we have carried out stable carbon and nitrogen isotope analysis of mandibular bulk bone collagen samples of four younger children (ca. 3 to 6 years) and one older child (ca. 7.5 years) of indeterminate sex, one male adolescent (ca. 18 years), and two male young adults (ca. 24 to 35 years). We have also analyzed incremental primary dentine collagen microsamples from their deciduous second and/or permanent first molars to reconstruct isotopic changes throughout infancy and childhood. Specifically, this study aims to determine whether individuals who died in childhood (< 12 years of age) (non-survivors) diverge isotopically from those who survived into adolescence and adulthood (survivors). This leads to an exploration of the reasons behind potential differences in infant and child rearing practices. Specifically, we investigate the presence of distinct parental dietary strategies and/or metabolic routing effects as a result of physiological stress.

## Material

Moro de Alins cave is located on the southern slopes of the Aragonese pre-Pyrenees of north-eastern Iberia, at its boundary with the Ebro valley, at 650 m above sea level. The environment is currently characterized by a continental Mediterranean climate with mean annual temperature between 12 and 14 °C and mean annual precipitation of ca. 500 mm. Access to the cave is along a 15-m narrow horizontal gallery facing northeast. The gallery leads to a long narrow passage with irregularly shaped limestone blocks, at the end of which there is a trapezoidal room less than half a meter wide at its entrance with a vertical 15-m deep well providing access to the lower level, which is also formed by another horizontal and narrow gallery (Pérez-Lambán et al. 2017) (Fig. 1).

The site has provided more than 800 commingled human skeletal remains corresponding to a minimum number of individuals (MNI) of 11, including four younger children (3–6 years), one older child (7–12 years), one male adolescent (13–19 years), and five young adults (20–39 years), comprising three males and two possible females (Alconchel 2017). The fact that individuals younger than 2 years are not represented in the cave is not surprising, as the exclusion of younger infants from the community's mortuary space is a common phenomenon archaeologically. The site has also provided a very rich material culture, including decorated pottery sherds and one complete undecorated vessel (Rodanés 2017b); two barbed and tanged bone arrowheads (Rodanés 2017c); some flint blades, one polished stone axe and two pebble hammers (Mazo 2017); two stone beads of variscite and blue *pasta vitrea* (Rodanés 2017d); twelve bronze and iron objects (including an axe, a dagger and a bronze arrowhead) (Rodanés et al. 2017a, b, c, d); and a number of extraordinarily well-preserved fragments of basketry and wooden objects, including a comb directly dated to 1730–1545 cal BC (3550 ± 30 BP, Beta-435577), a complete footed tray dated to 1660–1505 cal BC (3310 ± 30 BP, Beta-435575), two fragmented feet of a similar tray dated to 2030–1885 cal BC (3600 ± 30 BP, Beta-380266), and fragments of a large wooden vessel (Rodanés and Alcolea 2017a, 2017b; Alcolea and Rodanés 2019). Unfortunately, the vast majority of the material was recovered through clandestine excavations in 1991 and is completely decontextualized. While ranging from the Neolithic to Roman, a large part of the assemblage shows typological features or radiocarbon dates attributable to the Bronze Age (Rodanés 2017a). As part of this research, the eight mandibles available in the human skeletal collection were radiocarbon dated. All yielded Bronze Age dates (Table 1), modeled as lying between ca. 2030 and 1440 cal BC, with seven out of eight individuals falling in the first quarter of the 2nd millennium cal BC and the eighth (individual MOR4), some three centuries later.

While Moro de Alins Bronze Age burial cave cannot be associated with any specific habitation site, open-air sites (both in valley and hilltop locations) are abundant in the wider region, suggesting a relatively high population density. These small- and medium-sized settlements, occasionally walled, provide evidence of numerous undifferentiated wells, storage pits, and post-holes. Dwelling typologies were apparently diverse, including oval-shaped wattle-and-daub huts, square stone-masonry dwellings, and timber and
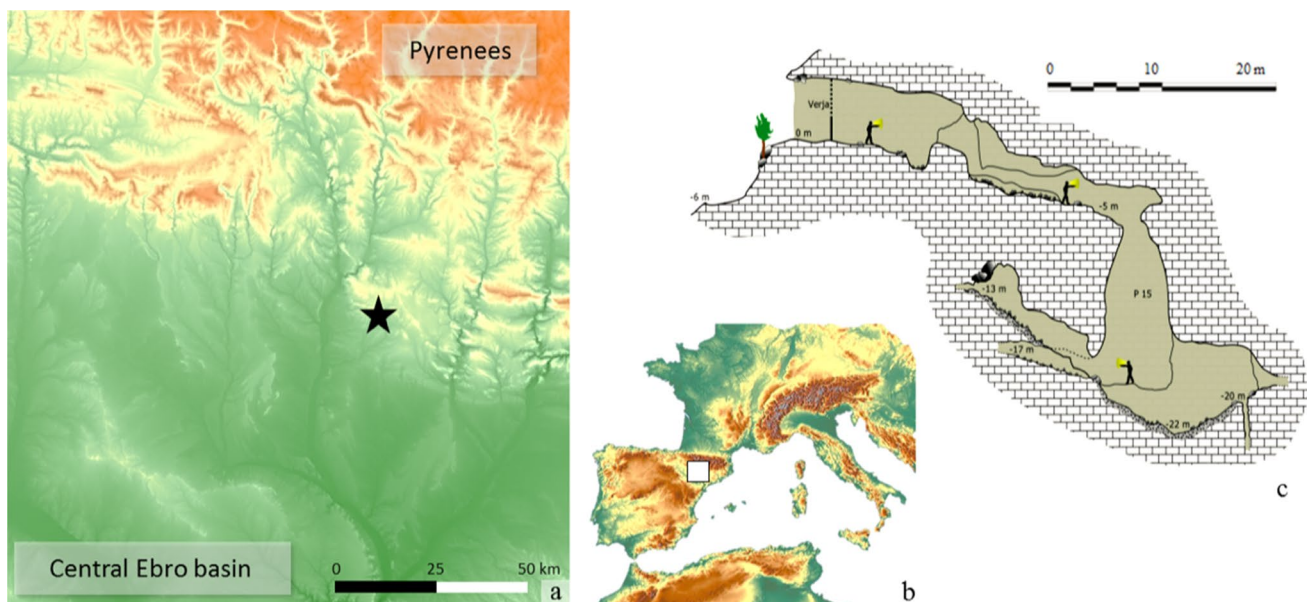


**Fig. 1** Location (**a**) (**b**) and topography (**c**) of Moro de Alins cave (Huesca, Spain). Topography: Aragon Speleology Centre (CEA). Modified from Alcolea and Rodanés (2019)

**Table 1** Calibrated radiocarbon dates of the individuals analyzed from Moro de Alins cave, using OxCal 4.2 (Bronk Ramsey 2009; Reimer et al. 2020)

| Inventory no | Individual | Age at death (years) | Sex[a] | Lab reference | $^{14}C$ (BP) | ± | cal. BC (95%) | | $\delta^{13}C$ (‰) |
|---|---|---|---|---|---|---|---|---|---|
| 12.09.220 | MOR7 | ca. 24–30 | M | OxA-V-3050-8 | 3591 | 28 | 2030 | 1882 | –18.99 |
| 12.09.354–355 | MOR5 | ca. 6 | I | OxA-V-3049-34 | 3567 | 20 | 2014 | 1783 | –18.78 |
| 12.09.82–83 | MOR2 | ca. 5.5 | I | OxA-V-3049-32 | 3548 | 20 | 1951 | 1775 | –18.82 |
| 12.09.213 | MOR10 | ca. 3 | I | OxA-V-3050-9 | 3527 | 28 | 1940 | 1751 | –19.45 |
| 12.09.423–424 | MOR6 | ca. 6 | I | OxA-V-3049-35 | 3488 | 20 | 1883 | 1746 | –19.49 |
| 12.09.199 | MOR11 | ca. 18 | M | OxA-V-3050-10 | 3469 | 27 | 1883 | 1694 | –19.12 |
| 12.09.358–359 | MOR3 | ca. 35 | M | OxA-V-3053-30 | 3468 | 21 | 1881 | 1696 | –19.31 |
| 12.09.336–337 | MOR4 | ca. 7.5 | I | OxA-V-3049-33 | 3232 | 21 | 1533 | 1443 | –19.79 |

[a]*M*, male; *I*, indeterminate

stone dwellings, which generally lack any internal divisions (Blanco-González et al. 2018). Subsistence relied on crop cultivation and sheep/goat and cattle herding, complemented with hunting and gathering. Production and trade of pottery and metal were key, consolidated activities in the local economy (Gallart et al. 2017). Little information is available on living conditions of north-eastern Iberian Bronze Age populations. Research usually refers to generally poor health marked by recurrent episodes of malnourishment, nutrient malabsorption, and infections mainly manifesting as enamel hypoplasia, oral pathologies, and non-specific periosteal or porotic reactions (e.g., Alconchel 2017; Etxeberria 1986; Rodanés et al. 2019). Similar findings in other Iberian regions have been related with difficult living conditions, especially during the first years of life (e.g., Nájera et al. 2010; Rubio 2021). Zoonotic diseases such as brucellosis and tuberculosis, resulting from close contact between domestic animals and humans; potential water-borne or poor hygiene-related diseases like diarrhea, potentially linked to suboptimal food and water storage; and oral infections, have been suggested to be among the main health hazards for both non-adults and adults together with nutritional deficiencies (Nájera et al. 2010; Rubio 2021). Once present, the transmission of disease would have been exacerbated by household crowding due to high fertility rates, cohabitation with domestic animals, and small-size dwellings, combined with few and narrow spaces to circulate between buildings and the scarcity of large, open communal spaces (Lull et al. 2013).

This study focuses on the isotope analysis of bulk bone and sequential dentine collagen of the deciduous second molar (whose formation spans, on average, from 30 weeks in utero to 3.5 years) and/or the permanent first molar (whose formation spans, on average, from birth to 10 years) from the eight radiocarbon dated mandibles, which show no or minimal dental attrition. The remaining three individuals identified in the MNI (one male and two possible female adults) are not represented by mandibles. The scarcity and poor preservation state of the human remains tentatively identified as female (i.e., a maxilla, a left parietal fragment, and a frontal bone fragment) preclude reliable sex estimation, and, therefore, they were excluded from sampling. This also applies to the male adult, which is only represented by temporal and occipital cranial fragments. Given the commingled state of the skeletal assemblage, age-at-death was estimated through tooth development in the case of juveniles and occlusal wear in the case of adults (AlQahtani et al. 2010; Brothwell 1981), while sex estimation was based on dimorphic mandibular traits (Brothwell 1981).

## Methods

### Bone collagen

Bone collagen was extracted from each mandibular sample following the protocol in Richards and Hedges (1999). Approximately, 0.8 g of pre-cleaned bone by air abrasion with aluminum oxide powder was demineralized in 10 ml aliquots of 0.5 M hydrochloric acid (HCl) at 4 °C for 1 week. The residue was then rinsed three times in deionized water before being gelatinized in pH 3 HCl at 72 °C for 48 h. The resulting solution was filtered with a 5–8 mm EZEE filter, with the supernatant then being lyophilized over a period of 24 h.

### Dentine collagen

Czermak et al.'s (2020) method was followed. Teeth were mechanically cleaned by air abrasion with aluminum oxide powder to remove surface debris, then partially embedded in Herculite II (a high-strength gypsum molding material) leaving one root's mesial or distal surface exposed to guide the cut, and sectioned to obtain a ~ 1.5-mm-wide mid-tooth longitudinal slice with a Buehler IsoMet low-speed diamond

saw. Then, each slice was demineralized in 10 ml aliquots of 0.5 M HCl at 4 °C for approximately 2 weeks and treated with 0.1 M NaOH for 30 min and 0.5 M HCl for 1 h at room temperature with thorough rinsing with deionized water between each reagent (cf. Brock et al. 2010). Subsequently, the tooth slices—still retaining their original shape—were rinsed in deionized MilliU water three times until pH neutral and sampled sequentially from crown to apical root using a 1-mm-diameter KAI Medical biopsy punch with plunger, avoiding secondary and tertiary dentine (i.e., pulp chamber and radicular channels) and cementum (i.e., outer root surface). Resulting dentine microsamples were labeled according to a numerical sequence of dentine segments and their approximate age assigned by comparing the dentine sections' anatomical location to the stage of dental development, following AlQahtani et al. (2010). Dentine microsamples were lyophilized without denaturing.

Both lyophilized bone collagen and dentine samples were weighed into tin capsules and loaded into a SERCON 20–22 continuous flow isotope ratio mass spectrometer coupled with an elemental analyzer at the Research Laboratory for Archaeology and the History of Art (RLAHA), University of Oxford.

Analytical precision is ± 0.2‰ (1σ) for $\delta^{13}$C and $\delta^{15}$N based on repeated analyses of in-house (alanine, marine seal, cow) and international standards (caffeine IAEA 600). Bone samples were measured in duplicate, while dentine collagen samples were not due to the relatively low yields (~ 0.5–0.7 mg) resulting from the sampling technique and to the impossibility of precisely replicating a sample elsewhere on the same tooth due to the complexity of primary dentine deposition (Nanci 2008).

Collagen preservation quality was checked according to standard criteria, including collagen yield, atomic weight C:N ratio, and %C and %N (Ambrose 1990; DeNiro 1985; van Klinken 1999). A more constrained C:N range of 3.1–3.3 rather than the oft cited 2.9–3.6 for bone collagen (DeNiro 1985; van Klinken 1999) was used for the dentine samples, given the lack of duplicate measurements. This more closely reflects the calculated C:N ratio of 3.2 for intact collagen (Szpak 2011). Recent work on fluorescence screening of collagen preservation in human primary dentine suggests that C:N ratios higher than 3.3 in non-denatured dentine samples indicate some degree of collagen decay or degradation, which may result in lower %N (Czermak et al. 2019). Finally, only samples weighing ≥ 0.35 mg were considered reliable, because lower weights may affect mass spectrometer measurements (e.g., Burt and Amin 2014).

## Statistical analysis

Statistical analysis of data was performed using SPSS v19. Shapiro–Wilk tests were used to assess whether the data were normally distributed. Levene's tests were used to assess homogeneity of variance. For two-sample comparisons (e.g.,

mean isotope values between groups of individuals), Student's $t$ tests were employed when the data did not depart significantly from a normal distribution; when they did, nonparametric Mann–Whitney $U$ tests were used. Depending on whether the data met the aforementioned two criteria, parametric one-way ANOVA or non-parametric Kruskal–Wallis tests were used to assess differences in mean dentine collagen isotope values by age categories between individuals. Two level mixed model nested ANOVA tests were used to assess variation in mean dentine collagen isotope ratios by age categories between individuals surviving and nonsurviving to age 10, because in this case the comparison involved one measurement variable (e.g., $\delta^{13}$C values) and two nominal variables (individual and survival to age 10 years), the latter being nested (i.e., forming subgroups within groups; McDonald 2014). Due to unequal group sample sizes, the Satterthwaite formula was applied, using modified mean squares at each level to provide a better estimate of the effective degrees of freedom and, therefore, more accurate $p$ values (Satterthwaite 1946). Z-scores were calculated to detect the presence of outliers where appropriate. A significance level of $\alpha = 0.05$ was used for all tests.

## Results

All bone collagen samples included in the study ($n = 8$) yielded good quality collagen (Table 2). Ten out of 187 dentine samples obtained from the deciduous second and permanent first molars failed to meet the criteria set out above, leaving 177 for analysis (Table S1). It is worth noting that only five out of these 177 samples (the first sample in each deciduous second molar analyzed) represent prenatal (i.e., fetal) life.

While bone collagen results are limited by the small sample size ($n = 8$), MOR4 exhibits lower $\delta^{13}$C and higher $\delta^{15}$N values than the other individuals (Z-score = 1.7 for both isotopes). This difference may have a chronological component, since MOR4 has the youngest radiocarbon date (Fig. 2). However, bone collagen isotope measurements average different periods of time depending on the biological age of the individual, and, thus, they can be impacted by physiological factors and/or age-specific diets (note that MOR4 is a child of ca. 7.5 years) and not necessarily diachronic shifts in subsistence practices. To confirm whether this individual is also an outlier in the dentine isotope data, we assessed the spread of individual dentine isotope values within five age categories (0–1.4, 1.5–2.9, 3–4.4, 4.5–5.9 and 6–7.4 years). The results of the Kruskal–Wallis and one-way ANOVA tests show significant differences between individuals in both $\delta^{13}$C and $\delta^{15}$N values in all age categories (0–1.4 years, $\delta^{13}$C: $F_{(7, 33)} = 4.6$, $p = 0.001$, $\delta^{15}$N: $\chi^2 = 25.4$, df = 7, $p = 0.001$; 1.5–2.9 years, $\delta^{13}$C: $\chi^2 = 35.8$, df = 7, $p < 0.001$, $\delta^{15}$N: $\chi^2 = 37.9$, df = 7,
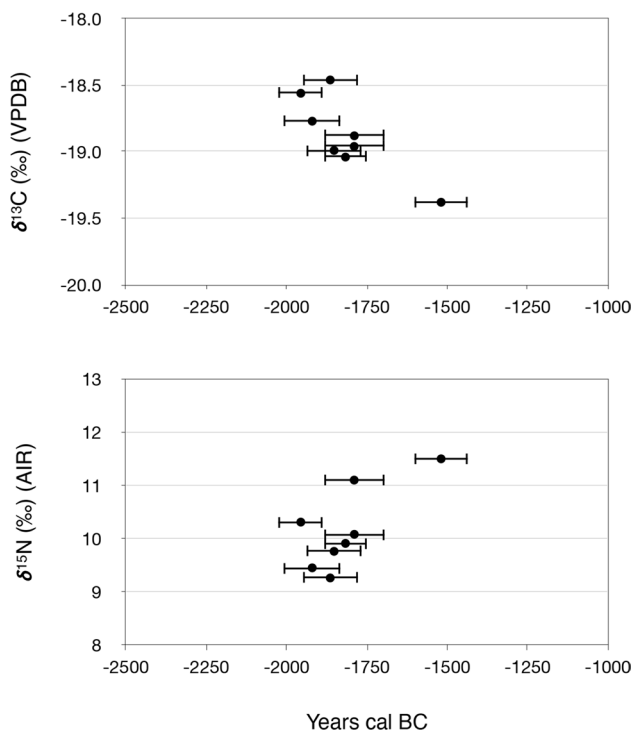
**Table 2** Mandibular bulk bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of the eight individuals analyzed from Moro de Alins cave

| Inventory no | Individual | Age at death (years) | Sex[a] | cal. BC (95%) | Yield | %C | %N | C:N | $\delta^{13}C$ (‰) (VPDB) | $\delta^{15}N$ (‰) (AIR) |
|---|---|---|---|---|---|---|---|---|---|---|
| 12.09.220 | MOR7 | ca. 24–30 | M | 2030–1882 | 14.3 | 43.3 | 15.6 | 3.2 | −18.6 | 10.3 |
| 12.09.354–355 | MOR5 | ca. 6 | I | 2014–1783 | 6.6 | 34.7 | 12.5 | 3.2 | −18.8 | 9.4 |
| 12.09.82–83 | MOR2 | ca. 5.5 | I | 1951–1775 | 12.9 | 41.9 | 15.2 | 3.2 | −18.5 | 9.3 |
| 12.09.213 | MOR10 | ca. 3 | I | 1940–1751 | 12.8 | 44.3 | 16.1 | 3.2 | −19.0 | 9.8 |
| 12.09.423–424 | MOR6 | ca. 6 | I | 1883–1746 | 7.3 | 44.1 | 15.8 | 3.3 | −19.0 | 9.9 |
| 12.09.199 | MOR11 | ca. 18 | M | 1883–1694 | 7.9 | 37.3 | 13.4 | 3.3 | −19.0 | 11.1 |
| 12.09.358–359 | MOR3 | ca. 35 | M | 1881–1696 | 13.7 | 42.1 | 15.3 | 3.2 | −18.9 | 10.1 |
| 12.09.336–337 | MOR4 | ca. 7.5 | I | 1533–1443 | 4.5 | 41.5 | 14.7 | 3.3 | −19.4 | 11.5 |

[a]*M*, male; *I*, indeterminate



**Fig. 2** Mandibular bulk bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of the eight individuals analyzed from Moro de Alins cave, plotted against calibrated radiocarbon dates (95%)

$p < 0.001$; 3–4.4 years, $\delta^{13}C$: $F_{(6, 19)} = 5.2$, $p = 0.003$, $\delta^{15}N$: $F_{(6, 19)} = 22.3$, $p < 0.001$; 4.5–5.9 years, $\delta^{13}C$: $F_{(5, 18)} = 45.7$, $p < 0.001$, $\delta^{15}N$: $F_{(5, 18)} = 22.5$, $p < 0.001$). These are mainly driven by individual MOR4, which *post hoc* tests confirm as a clear outlier throughout their entire early-life isotope sequence, as supported by statistically significant differences in $\delta^{13}C$ and $\delta^{15}N$ values with the rest of the individuals in 8 out of 23 and 20 out of 23 possible pairwise comparisons, respectively (Table 3). Consistent with bone collagen results, this individual shows lower $\delta^{13}C$ and especially higher $\delta^{15}N$ ratios practically from birth, offering support for a diachronic interpretation. Leaving MOR4 aside, there

also exists some variation in mean values between individuals, particularly MOR2 (a child of ca. 5.5 years of age) and MOR11 (an adolescent of ca. 18 years of age), who show significant differences in $\delta^{13}C$ values in 8 out of 16 possible pairwise comparisons to other contemporaneous individuals, showing higher and lower mean $\delta^{13}C$ values, respectively.

The beginning of the isotopic profiles of the deciduous second molars, which provide values for the last months of prenatal life (> 30 weeks in utero) and a finer temporal resolution than permanent first molars for the first 6 months of postnatal life, show a concomitant increase both in $\delta^{13}C$ and $\delta^{15}N$ values in at least the first two or three dentine microsamples that capture the start of breastfeeding at birth. The exception is, again, MOR4, who shows an unexpected pattern of opposing covariance of increasing $\delta^{13}C$ and decreasing $\delta^{15}N$ values from the first (prenatal) to the second (postnatal) dentine microsamples (Fig. 3), potentially attributable to anabolic change in utero. The first dentine microsamples from the permanent first molars, as expected, show elevated values for both isotopes indicative of high-trophic-level dietary protein intake characteristic of exclusive breastfeeding, because their formation starts around birth.

Isotope values compatible with exclusive breastfeeding are estimated as persisting for ca. $0.3 \pm 0.2$ years (Table 4), with no differences in duration detected between survivors and non-survivors. However, it is worth noting that there are at least two individuals whose isotope profiles show patterns of opposing covariance during this period, which complicates the estimation of the exclusive nursing period (i.e., MOR2 around age 0.5, and MOR6 from 0.1 to 0.7 years). In those cases, $\delta^{13}C$ values are preferentially used as a guide of weaning events because they may be less susceptible to physiological stress (e.g., Beaumont et al. 2018). Isotope values compatible with exclusive breastfeeding (Table 4) show a mean trophic enrichment of ca. 1.0‰ and 3.1‰, respectively, in comparison with mean adult bone collagen values (i.e., $\delta^{13}C = −18.8 \pm 0.2$‰ and $\delta^{15}N = 10.5 \pm 0.5$‰, $n = 3$, Table 2), which, despite the lack of adolescent or

**Table 3** P values of *post hoc* Dunn–Bonferroni and Tukey tests applied to compare dentine carbon ($\delta^{13}C_{dcol}$) and nitrogen ($\delta^{15}N_{dcol}$) isotope values between individuals, by age category

| Individual | Age category[a] (years) | $\delta^{13}C$ (‰) (VPDB) | | | | | | | $\delta^{15}N$ (‰) (AIR) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | MOR3 | MOR4 | MOR5 | MOR6 | MOR7 | MOR10 | MOR11 | MOR3 | MOR4 | MOR5 | MOR6 | MOR7 | MOR10 | MOR11 |
| MOR2 | 0.0–1.4[b] | 0.535 | **0.011** | **0.025** | 0.352 | **0.035** | 0.081 | 0.214 | 0.995 | **0.006** | 0.098 | 1.000 | 1.000 | 0.229 | 1.000 |
| | 1.5–2.9[b] | 0.823 | 0.806 | 0.115 | **0.002** | 0.525 | **<0.001** | **<0.001** | 0.608 | **0.008** | 1.000 | 0.920 | 1.000 | **0.012** | 0.643 |
| | 3.0–4.4[c] | 0.943 | **0.003** | **0.036** | 0.095 | 0.204 | — | 0.295 | 0.887 | **<0.001** | 1.000 | 0.429 | 0.179 | — | 0.553 |
| | 4.5–5.9[b] | **0.001** | **<0.001** | 0.342 | — | 0.147 | — | **<0.001** | 0.677 | **0.031** | 1.000 | — | 0.135 | — | 0.747 |
| MOR3 | 0.0–1.4[b] | | 1.000 | 0.999 | 1.000 | 1.000 | 0.899 | 0.759 | | **0.033** | **0.045** | 1.000 | 0.968 | 0.143 | 1.000 |
| | 1.5–2.9[b] | | 1.000 | 0.865 | 0.078 | 1.000 | **0.009** | **0.013** | | **0.026** | 0.577 | 0.994 | 0.772 | 1.000 | 0.998 |
| | 3.0–4.4[c] | | **0.014** | 0.160 | 0.332 | 0.689 | — | 0.806 | | **<0.001** | 0.934 | 0.060 | **0.007** | — | 0.053 |
| | 4.5–5.9[b] | | **0.049** | 0.405 | — | 0.407 | — | **0.026** | | **0.001** | 0.573 | — | **0.003** | — | **0.035** |
| MOR4 | 0.0–1.4[b] | | | 0.955 | 1.000 | 0.901 | 0.652 | 0.524 | | | **<0.001** | 0.399 | 0.137 | **0.011** | 0.436 |
| | 1.5–2.9[b] | | | 1.000 | 0.208 | 1.000 | **0.016** | **0.001** | | | **<0.001** | **<0.001** | **0.003** | **<0.001** | **<0.001** |
| | 3.0–4.4[c] | | | 0.983 | 0.978 | 0.233 | — | 0.234 | | | **<0.001** | **<0.001** | **0.002** | — | **<0.001** |
| | 4.5–5.9[b] | | | 0.109 | — | **0.046** | — | 0.832 | | | **0.049** | — | 0.087 | — | **0.019** |
| MOR5 | 0.0–1.4[b] | | | | 1.000 | 1.000 | 0.997 | 0.934 | | | | 0.308 | 0.843 | 0.836 | 1.807 |
| | 1.5–2.9[b] | | | | 0.260 | 0.997 | **0.010** | **<0.001** | | | | 0.798 | 1.000 | **<0.001** | 0.374 |
| | 3.0–4.4[c] | | | | 1.000 | 0.830 | — | 0.798 | | | | 0.366 | 0.138 | — | 0.470 |
| | 4.5–5.9[b] | | | | — | — | — | — | | | | — | — | — | — |
| MOR6 | 0.0–1.4[b] | | | | | 1.000 | 0.910 | 0.733 | | | | | 0.994 | 0.150 | 1.000 |
| | 1.5–2.9[b] | | | | | 0.142 | 0.329 | **<0.001** | | | | | 0.994 | 0.248 | 1.000 |
| | 3.0–4.4[c] | | | | | 0.943 | — | 0.923 | | | | | 1.000 | — | 0.998 |
| | 4.5–5.9[b] | | | | | — | — | — | | | | | — | — | — |
| MOR7 | 0.0–1.4[b] | | | | | | 0.970 | 0.794 | | | | | | 0.458 | 1.000 |
| | 1.5–2.9[b] | | | | | | **0.018** | **0.017** | | | | | | 0.078 | 0.834 |
| | 3.0–4.4[c] | | | | | | — | — | | | | | | — | — |
| | 4.5–5.9[b] | | | | | | 1.000 | 0.090 | | | | | | 0.101 | 0.605 |
| MOR10 | 0.0–1.4[b] | | | | | | | 1.000 | | | | | | | 0.483 |
| | 1.5–2.9[b] | | | | | | | 0.215 | | | | | | | 0.290 |
| | 3.0–4.4[c] | | | | | | | 1.000 | | | | | | | 0.986 |
| | 4.5–5.9[b] | | | | | | | **0.034** | | | | | | | 0.550 |

[a] The use of 1.5-year age categories is intended to capture feeding stages as best as possible, while ensuring enough sample sizes (at least, five individuals with ≥ 2 values each) to conduct statistical analyses

[b] *Post hoc* Dunn–Bonferroni test applied under the assumption of unequal variances for samples within 0–1.4 and 1.5–2.9 age categories

[c] *Post hoc* Tukey test applied under the assumption of equal variances for samples within 3–4.9 and 5–6.9 age categories

adult female mandibles to be used as a putative maternal baseline, is broadly consistent with the generally accepted trophic level offsets expected between exclusively breast-feeding infants and their mothers (i.e., $\Delta^{13}C \sim 1‰$ and $\Delta^{15}N \sim 2–3‰$; Fuller et al. 2006).

However, this general picture does not preclude inter-group variability. Thus, MOR4 shows clearly higher $\delta^{15}N$ values (15.8‰) than the other individuals (ca. 12–14‰), reinforcing its identification as an outlier. Differences in mean $\delta^{13}C$ values estimated to be compatible with exclusive breastfeeding that approach but do not quite attain statistical significance ($t = 2.467$, df = 5, $p = 0.057$, excluding MOR4) are seen between survivors (i.e., MOR3, MOR7 and MOR11; $-18.1 \pm 0.3‰$) and non-survivors (MOR2, MOR5, MOR6 and MOR10; $-17.6 \pm 0.2‰$). This results in significantly different mean $\Delta^{13}C$ trophic shifts compared to mean adult bone collagen $\delta^{13}C$ values between survivors (0.7‰) and non-survivors (1.2‰) ($t = 4.641$, df = 5, $p = 0.006$).

The weaning process is isotopically characterized by a mostly synchronic and sustained concomitant decrease in $\delta^{13}C$ and $\delta^{15}N$ values, falling a full trophic level on average after the complete cessation of nursing ($1.0 \pm 0.3‰$ for $\delta^{13}C$ and $3.7 \pm 0.5‰$ for $\delta^{15}N$) (Table 5). This process is isotopically traceable from $0.3 \pm 0.2$ years, as aforementioned, to $2.6 \pm 0.7$ years (Table 4), with no differences between survivors and non-survivors (whether excluding MOR4 or not). Despite the differences in temporal resolution, it is noteworthy that in all cases where both teeth were analyzed from the same individual (i.e., MOR2, MOR4, and MOR5), the isotope profiles were remarkably consistent (Fig. 3).

Excluding MOR4 as a clear outlier, individuals who survived into adolescence or adulthood show significantly different mean $\Delta^{13}C$ trophic shifts between exclusive breast-feeding and fully weaned ($0.7 \pm 0.2‰$) than non-survivors ($1.2 \pm 0.1‰$) ($t = 4.641$, df = 5, $p = 0.006$) (Table 5). Here again, this pattern is caused by the aforementioned difference in exclusive breastfeeding mean $\delta^{13}C$ values, since both groups show similar fully weaned mean $\delta^{13}C$ values ($-18.7 \pm 0.4‰$ vs. $-18.8 \pm 0.3‰$, respectively). Mean $\Delta^{15}N$ trophic shifts are similar between survivors and non-survivors ($3.5 \pm 0.7$ and $3.6 \pm 0.5‰$, respectively), consistent with no significant difference in mean $\delta^{15}N$ values between groups either during exclusive breastfeeding ($13.4 \pm 0.1‰$ vs. $13.2 \pm 0.6‰$) or when fully weaned ($9.9 \pm 0.6‰$ vs. $9.5 \pm 0.5‰$). Reconstructed sequential isotope profiles suggest variability in the rapidity of the transition from breast-milk to solid food, with a similar number of cases of gradual (MOR4, MOR5, MOR7, and MOR11) and abrupt (MOR2, MOR3 and, especially, MOR6 and MOR10) weaning. This variability does not correlate with the $^{14}C$ chronology of the individuals.

The post-weaning period is characterized by the presence of a number of patterns of opposing covariance characteristic of catabolic processes, observable as rising $\delta^{15}N$ and falling or stable $\delta^{13}C$ in the isotope profiles (Beaumont et al. 2018; Neuberger et al. 2013). These patterns are clearly visible at the end of the isotope profiles of MOR2 (from age 4 years onwards; age at death ca. 5.5 years), MOR4 (from age 6 years onwards; age at death ca. 7.5 years), MOR 6 (from age 2.5 years to, at least, 3.5 years; age at death ca. 6 years), and MOR10 (from age 1.5 years onwards; age at death ca. 3 years). Moreover, there are other possible instances—with lower temporal resolution—at the end of the isotope profile of MOR3 (from age 8.5 to 9.5 years; age at death ca. 35 years), three more along MOR7's profile (around age 4 years, from age 5 to 6 years, and possibly around age 7 years; age at death ca. 24–30 years), and another in the profile of MOR11 (from age 5 to 6 years; age at death ca. 18 years). We have one example of the contrary pattern characteristic of anabolic change (or of a shift in subsistence, such as increased $C_4$ consumption), observable as rising $\delta^{13}C$ and stable $\delta^{15}N$ in the early isotope profile of MOR11 (from age 3 to 4 years; age at death ca. 18 years). There is also evidence of a notable isotopic shift consistent with dietary change, where $\delta^{13}C$ and $\delta^{15}N$ values covary, at the end of the isotope sequence of MOR5 (from age 3.5 years onwards; age at death ca. 6 years).

Finally, comparing sequential dentine collagen $\delta^{13}C$ and $\delta^{15}N$ isotope values by age categories between non-survivors (either including or excluding MOR4) and survivors to age 10 years (when the first permanent molar stops forming) through a mixed model nested ANOVA test shows no statistically significant differences, despite the fact that mean $\delta^{13}C$ and $\delta^{15}N$ values seem to be consistently lower in most age categories among the survivors (Table 6). That being said, we must recall the small and unequal sample sizes available for comparison by individual and age category. The interpretative constraint of sample size is a common problem in micro-sequential dentine isotope studies due to material availability, curational concerns and funding limitations, so the potential impact of the small sample size on the robustness of the results should be always considered.

# Discussion

## Diachronic and synchronic isotopic differences between individuals

Diachronic differences detected in both bone and dentine collagen $\delta^{13}C$ and, especially, $\delta^{15}N$ values between MOR4 and the other individuals suggest changes in infant and child

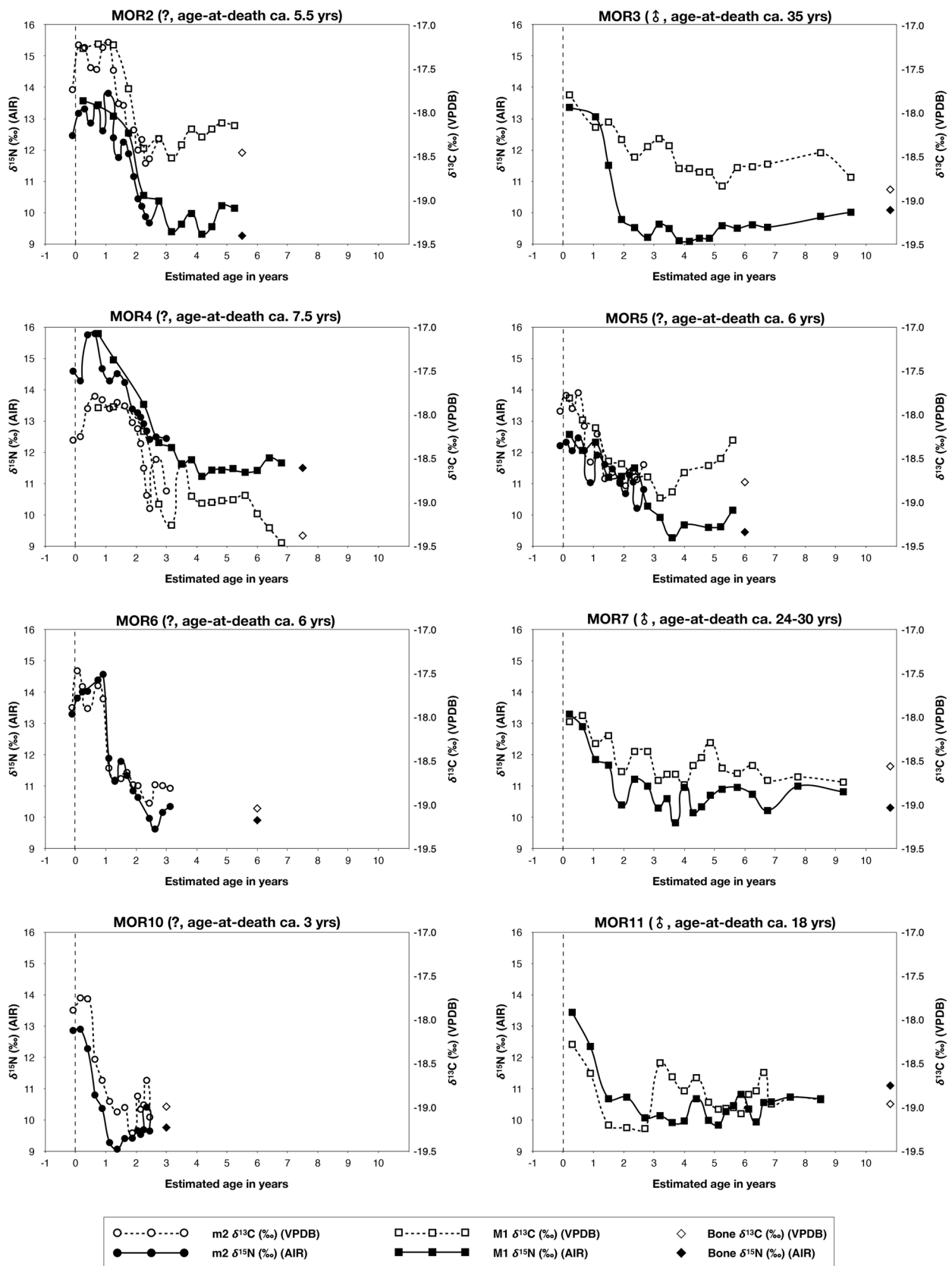**Fig. 3** Sequential dentine collagen δ¹³C and δ¹⁵N isotope profiles of the eight individuals analyzed from Moro de Alins cave. Mandibular bulk bone collagen isotope values are also plotted for reference

feeding practices within the Middle Bronze Age at Moro de Alins. However, the small sample size precludes drawing any strong conclusions. Differences in gender, social standing, health status, geographic origin, and/or subsistence practices may have also existed between MOR4 and the other individuals regardless of chronology.

Synchronic differences in $\delta^{13}C$ values were detected between contemporaneous individuals, particularly affecting MOR2 and MOR11, who, respectively, show higher and lower mean isotope values than the others in a number of age categories. The fact that differences are not consistently sustained across different age categories makes it difficult to assess whether or not this variability relates to differential parenting and/or subsistence strategies within the same community.

## Isotopic insights into the exclusive breastfeeding period

Stable isotope insights into exclusive breastfeeding are essentially based on raised $\delta^{15}N$ and $\delta^{13}C$ values in early life. All individuals at Moro de Alins show isotopic evidence of breastfeeding, and the period interpreted as exclusive nursing ($0.3 \pm 0.2$ years, i.e., $3.6 \pm 2.4$ months) may be understood as short. Current recommended infant feeding practices suggest exclusive nursing for the first 6 months of life as biologically optimal (Kramer and Kakuma 2004). Modern observational studies of LMIC have shown that, in the first 6 months of life, the relative risks of diarrhea and pneumonia morbidity and mortality for infants predominantly, partially or not breastfed, are significantly increased compared with those exclusively breastfed (Bahl et al. 2005; Briend et al. 1988). Suboptimal breastfeeding, especially non-exclusive breastfeeding in the first 6 months of life, is currently estimated to result in 1.4 million deaths and 10% of disease burden in children younger than 5 years worldwide (Black et al. 2008). Despite obvious differences in technology, medical care, lifestyle and population density between present-day LMIC and Iberian Bronze Age populations, it may be assumed that the short duration of exclusive breastfeeding at Moro de Alins might have caused higher rates of infant and child death and disease burden than if exclusive weaning had lasted longer. Breast milk insufficiency and return to work are the main reasons cited for the cessation of exclusive breastfeeding in present-day LMIC (e.g., Lakati et al. 2002). Although we cannot draw any direct comparisons, it is not improbable that Bronze Age women played a key role in subsistence strategies beyond the domestic sphere (e.g., farming, herding, manufacturing pottery or

textiles) that may have interfered with optimal exclusive breastfeeding practices. However, cultural understandings of nutrition and health or religious beliefs may also be behind reduced period of exclusive breastfeeding (e.g., Fouts 2004).

The detection of isotopic patterns of opposing covariance attributable to catabolic processes suggesting physiological stress during exclusive or nearly exclusive breastfeeding is possible, albeit difficult. The characteristic high $\delta^{15}N$ and $\delta^{13}C$ values for this period as a result of the trophic level effect of nursing would mask such signals. However, if there is both protein and lipid catabolism during breastfeeding, $\delta^{15}N$ values would rise further, while $\delta^{13}C$ values would decrease. There are at least two individuals whose isotope profiles show patterns of opposing covariance during the predominant breastfeeding period (MOR2 around age 0.5 years, i.e., 6 months, and MOR6 from 0.1 to 0.7 years, i.e., from 1.2 to 8.4 months). Despite the equifinality of such a pattern, this may suggest the mediation of a physiological factor, potentially related to malnutrition or disease (e.g., Fuller et al. 2005; Neuberger et al. 2013). The effects of poor-quality complementary foods and infectious diseases on infant development seem to be of roughly equal importance in present-day LMIC settings (e.g., Becker et al. 1991). However, nutritional stress during predominant breastfeeding, if present, would more likely derive from micronutrient deficiencies (due to maternal deficiencies and/or longitudinal decreases in breast milk concentrations of iron, zinc, calcium and vitamins D and $B_{12}$) than from macronutrient deficiencies, which, after a sharp decrease in the first weeks, remain relatively constant, especially with regard to milk intake and infant body weight ratio (Dror and Allen 2018). Variation in micronutrient levels within the required range to support body maintenance and growth is unlikely to alter $\delta^{15}N$ and $\delta^{13}C$ values, as opposed to variation in macronutrients such as protein and carbohydrates. Therefore, it is likely that the patterns of opposing covariance attributed to catabolic changes in the predominantly breastfed individuals are the result of infectious disease potentially associated poor hygiene, such as diarrhea. The latter adversely affects both growth and nutritional status, especially in very young individuals with immature immune systems (e.g., Black et al. 2008). Recurrent infections and/or growth flattening may also be behind a possible return to exclusive or nearly exclusive breastfeeding in MOR2 until age 0.7 years (i.e., 8.4 months) and MOR5 until age 0.5 years (i.e., 6 months), after a very early introduction of complementary foods around age 0.3 and 0.1 years (i.e., 3.6 and 1.2 months), respectively.

**Table 4** Estimated duration of exclusive breastfeeding and weaning processes, and age at complete weaning, for the studied individuals of Moro de Alins cave

| Inventory no | Individual/tooth | Age at death (years) | Sex[a] | Estimated duration of exclusive breastfeeding (years) | Estimated duration of the weaning process (years) | Age at complete weaning (years) |
|---|---|---|---|---|---|---|
| 12.09.82–83 | MOR2_m2 | ca. 5.5 | I | 0.3 | 2.1 | 2.4 |
| | MOR2_M1 | | | 0.3 | 2.0 | 2.3 |
| 12.09.336–337 | MOR4_m2 | ca. 7.5 | I | 0.6 | Indet | Indet |
| | MOR4_M1 | | | 0.8 | 2.7 | 3.5 |
| 12.09.354–355 | MOR5_m2 | ca. 6 | I | 0.1 | Indet | Indet |
| | MOR5_M1 | | | 0.2 | 3.4 | 3.6 |
| 12.09.423–424 | MOR6_m2 | ca. 6 | I | 0.1 | 2.5 | 2.6 |
| 12.09.213 | MOR10_m2 | ca. 3 | I | 0.2 | 1.2 | 1.4 |
| *Non-survivors[b]* | | | *Mean* | *0.3* | *2.4* | *2.7* |
| | | | *σ* | *0.2* | *0.8* | *0.9* |
| *Non-survivors, with MOR4 excluded as an outlier[b]* | | | *Mean* | *0.2* | *2.3* | *2.5* |
| | | | *σ* | *0.1* | *0.9* | *0.9* |
| 12.09.358–359 | MOR3_M1 | ca. 35 | M | 0.2 | 2.6 | 2.8 |
| 12.09.220 | MOR7_M1 | ca. 24–30 | M | 0.2 | 1.7 | 1.9 |
| 12.09.199 | MOR11_M1 | ca. 18 | M | 0.3 | 2.4 | 2.7 |
| *Survivors* | | | *Mean* | *0.2* | *2.2* | *2.5* |
| | | | *σ* | *0.1* | *0.5* | *0.5* |
| *All results combined[b]* | | | *Mean* | *0.3* | *2.3* | *2.6* |
| | | | *σ* | *0.2* | *0.7* | *0.7* |

[a]*M*, male; *I*, indeterminate

[b]When both m2 and M1 values are available for the same individual (i.e., MOR2, MOR4 and MOR5), their average is taken and used to calculate the mean and standard deviation

## Isotopic insights into the weaning period

Isotopic insights into weaning are essentially based on declining $\delta^{15}N$ and $\delta^{13}C$ values between the estimated onset and cessation of breastfeeding. The age at the completion of weaning at Moro de Alins ($2.6 \pm 0.7$ years) is comparable to most traditional societies (Jay 2009). The two exceptions are MOR4, with a cessation of breastfeeding estimated around age 3.5 years, and MOR10, estimated around age 1.4 years. In the first case, the significantly longer duration of nursing may relate to diachronic socio-economic or cultural changes in infant and child feeding practices over the Bronze Age. Differences in rearing due to gender, health status, social position, or geographic origin may have also existed between MOR4 and the other individuals, though we have no evidence with which to further address these possibilities. In the second case, the rationale behind the shorter and more abrupt weaning process detected in MOR10 is even more difficult to address with the archeological information available. Whatever the case, this short weaning process may have negatively impacted the life expectancy of MOR10, who died around 3 years of age.

Together with inadequate hygiene, suboptimal feeding (in both frequency and nutrient density) is a clear determinant of infant morbidity and mortality. Regular breastmilk consumption and high-quality complementary food intake, including sufficient micro- and macro-nutrients, is essential for optimal growth, especially in the first 2 years of life when infants have a high nutrient demand (e.g., Dewey et al. 1992). In this regard, it is noteworthy that in the Moro de Alins sample, there are statistically significant differences in $\Delta^{13}C$ trophic shifts from exclusive breastfeeding to fully weaned (and to mean adult bone collagen $\delta^{13}C$ values) between individuals who survived into late adolescence or adulthood and those who did not. Survivors show shifts ($0.7 \pm 0.2$‰, ranging 0.5 to 0.9‰, $n = 3$) that are broadly consistent with published modern mother-infant trophic distances published (Fuller et al. 2006; Herrscher et al. 2017). By contrast, non-survivors (with MOR4 excluded as an outlier) show significantly higher trophic shifts ($1.2 \pm 0.1$‰, ranging 1.1 to 1.3‰, $n = 5$) that are above most of the modern mother-infant trophic distances. Only 3 out of 23 published modern mother-infant pairs have $\delta^{13}C$ trophic shifts that exceed 1‰ (Fogel et al. 1989; Fuller et al. 2006; Herrscher et al. 2017), despite the recurrent use in paleodietary literature of ~1‰ as the theoretically acceptable mean mother-infant $\Delta^{13}C$ based on Fuller et al. (2006). Thus, it may be tentatively proposed that individuals who consumed more

**Table 5** $\delta^{13}C$ and $\delta^{15}N$ values estimated to be compatible with fetal life right before birth, with exclusive breastfeeding and with fully weaned, and trophic distances between both exclusive breastfeeding and fully weaned, for the studied individuals from Moro de Alins cave

| Inventory no | Individual/tooth | Age at death (years) | Sex[a] | $\delta^{13}C$ (‰) fetal life[b] | $\delta^{13}C$ (‰) exclusive breastfeeding[c] | $\delta^{13}C$ (‰) fully weaned[d] | $\Delta^{13}C_{\text{exclusive breastfeeding-fully weaned}}$ | $\delta^{15}N$ (‰) fetal life[b] | $\delta^{15}N$ (‰) exclusive breastfeeding[c] | $\delta^{15}N$ (‰) fully weaned[d] | $\Delta^{15}N_{\text{exclusive breastfeeding-fully weaned}}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 12.09.82–83 | MOR2_m2 | ca. 5.5 | I | −17.7 | −17.3 | −18.5 | 1.2 | 12.5 | 13.3 | 9.7 | 3.6 |
|  | MOR2_M1 |  |  | – | −17.3 | −18.4 | 1.1 | – | 13.6 | 10.6 | 3.0 |
| 12.09.336–337 | MOR4_m2 | ca. 7.5 | I | −18.3 | −17.8 | – | – | 14.6 | 15.8 | – | – |
|  | MOR4_M1 |  |  | – | −17.9 | −18.6 | 0.7 | – | 15.8 | 11.6 | 4.2 |
| 12.09.354–355 | MOR5_m2 | ca. 6 | I | −18.0 | −17.8 | – | – | 12.2 | 12.3 | – | – |
|  | MOR5_M1 |  |  | – | −17.8 | −18.9 | 1.1 | – | 12.6 | 9.3 | 3.3 |
| 12.09.423–424 | MOR6_m2 | ca. 6 | I | −17.9 | −17.5 | −18.8 | 1.3 | 13.3 | 13.8 | 9.6 | 4.2 |
| 12.09.213 | MOR10_m2 | ca. 3 | I | −17.9 | −17.8 | −19.1 | 1.3 | 12.9 | 12.9 | 9.1 | 3.8 |
| *Non–survivors[e]* |  |  | *Mean* | *−18.0* | *−17.7* | *−18.8* | *1.1* | *13.1* | *13.7* | *10.0* | *3.7* |
|  |  |  | *σ* | *0.2* | *0.2* | *0.3* | *0.2* | *0.9* | *1.3* | *1.0* | *0.5* |
| *Non–survivors, with MOR4 excluded as an outlier[e]* |  |  | *Mean* | *−17.9* | *−17.6* | *−18.8* | *1.2* | *12.7* | *13.2* | *9.5* | *3.6* |
|  |  |  | *σ* | *0.1* | *0.2* | *0.3* | *0.1* | *0.5* | *0.6* | *0.5* | *0.5* |
| 12.09.358–359 | MOR3_M1 | ca. 35 | M | – | −17.8 | −18.4 | 0.6 | – | 13.4 | 9.2 | 4.2 |
| 12.09.220 | MOR7_M1 | ca. 24–30 | M | – | −18.1 | −18.6 | 0.5 | – | 13.3 | 10.4 | 2.9 |
| 12.09.199 | MOR11_M1 | ca. 18 | M | – | −18.3 | −19.2 | 0.9 | – | 13.4 | 10.1 | 3.3 |
| *Survivors* |  |  | *Mean* | – | *−18.1* | *−18.7* | *0.7* | – | *13.4* | *9.9* | *3.5* |
|  |  |  | *σ* | – | *0.3* | *0.4* | *0.2* | – | *0.1* | *0.6* | *0.7* |
| *All results combined[e]* |  |  | *Mean* | – | *−17.8* | *−18.8* | *1.0* | – | *13.6* | *9.9* | *3.7* |
|  |  |  | *σ* | – | *0.3* | *0.3* | *0.3* | – | *1.0* | *0.8* | *0.5* |

[a] *M*, male; *I*, indeterminate

[b] Corresponding to the, in this case, unique isotope value available before birth in the isotope profiles of the m2s studied

[c] Corresponding to the highest isotope value compatible with exclusive breastfeeding

[d] Corresponding to the lowest isotope value compatible with the cessation of breastfeeding

[e] When both m2 and M1 values are available for the same individual (i.e., MOR2, MOR4, and MOR5), their average is taken and used to calculate the mean and standard deviation

**Table 6** Comparison of dentine collagen mean carbon ($\delta^{13}C_{dcol}$) and nitrogen ($\delta^{15}N_{dcol}$) isotope values between survivors and non-survivors to age 10, by age category

| Age category[a] (years) | Non-survivors | | | | Survivors | | | | Mixed model nested ANOVA[d] | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $k$[b] | $n$[b] | pooled mean | $\sqrt{GV}$[c] | $k$[b] | $n$[b] | pooled mean | $\sqrt{GV}$[c] | $F$ | $p$ |
| $\delta^{13}C_{dcol}$ (‰) (VPDB) | | | | | | | | | | |
| 0.0–1.4 | 5 | 34 | −18.0 | 0.5 | 3 | 7 | −18.2 | 0.3 | $F_{(1, 8)} = 0.57$ | 0.476 |
| 1.5–2.9 | 5 | 54 | −18.5 | 0.5 | 3 | 11 | −18.7 | 0.4 | $F_{(1, 7)} = 0.23$ | 0.650 |
| 3.0–4.4 | 4 | 12 | −18.7 | 0.3 | 3 | 13 | −18.6 | 0.1 | $F_{(1, 5)} = 0.77$ | 0.429 |
| 4.5–5.9 | 3 | 11 | −18.5 | 0.4 | 3 | 13 | −18.7 | 0.2 | $F_{(1, 4)} = 0.57$ | 0.504 |
| Combined (0.0–5.9) | 5 | 111 | −18.4 | 0.5 | 3 | 44 | −18.6 | 0.3 | $F_{(1, 6)} = 1.18$ | 0.320 |
| $\delta^{15}N_{dcol}$ (‰) (AIR) | | | | | | | | | | |
| 0.0–1.4 | 5 | 34 | 12.8 | 1.6 | 3 | 7 | 12.9 | 0.6 | $F_{(1, 7)} = 0.01$ | 0.918 |
| 1.5–2.9 | 5 | 54 | 11.3 | 1.5 | 3 | 11 | 10.5 | 0.8 | $F_{(1, 7)} = 1.03$ | 0.349 |
| 3.0–4.4 | 4 | 12 | 10.4 | 1.2 | 3 | 13 | 10.0 | 0.6 | $F_{(1, 5)} = 0.66$ | 0.461 |
| 4.5–5.9 | 3 | 11 | 10.3 | 0.9 | 3 | 13 | 10.1 | 0.6 | $F_{(1, 4)} = 0.15$ | 0.728 |
| Combined (0.0–5.9) | 5 | 111 | 11.6 | 1.7 | 3 | 44 | 10.6 | 1.2 | $F_{(1, 6)} = 2.14$ | 0.194 |

[a]The use of 1.5-year age categories is intended to capture feeding stages as best as possible, while ensuring enough sample sizes ($n \geq 5$ and, at least, two individuals represented by group) to conduct statistical analyses

[b]$k$ = no. individuals; $n$ = no. samples

[c]Composite or pooled standard deviations

[d]Satterthwaite's correction formula is used to take into account unequal group sample sizes (McDonald 2014; Satterthwaite 1946)

(isotopically) similar foods to their mothers during the weaning period (and beyond) had greater chances of survival. The fact that the larger $\Delta^{13}C$ trophic shifts among non-survivors in Moro de Alins are mainly due to their higher exclusive breastfeeding mean $\delta^{13}C$ values, with no accompanying difference in $\Delta^{15}N$ trophic shifts or in exclusive breastfeeding mean $\delta^{15}N$ values, may indicate some contribution of $C_4$ plants, such as millet (present in the Iberian Bronze Age; Moreno-Larrazabal et al. 2015), to non-survivors' maternal diet, possibly suggesting unequal family access to certain food resources.

Another explanation may invoke maternal and/or infant physiological stress exclusively. In this scenario, an increase in $\delta^{15}N$ values as a result of protein catabolism and a potential decrease in $\delta^{13}C$ values as a result of lipid catabolism would theoretically be expected among malnourished and/or ill children. It is likely, however, that opposite compensating effects between dietary and metabolic changes have masked $\delta^{15}N$ and $\delta^{13}C$ disparities and instances of opposing covariance (catabolic change) thus preventing detection of existing protein and/or calorie deficits during exclusive breastfeeding and/or weaning among non-survivors. For example, a $\delta^{15}N$ increase due to muscle wasting resulting from severe protein malnutrition during weaning would be blurred by an antagonistic $\delta^{15}N$ decrease from the introduction of low-trophic-level cereals (Dailey-Chwalibóg et al. 2020), especially while maternal breastmilk still provided from one-third to half of a child's energy needs. Similarly, a

metabolic decrease in $\delta^{13}C$ values may be partially blurred by an overlapping decrease as a result of the introduction of complementary foods of lower trophic level. Moreover, in the case of $\delta^{13}C$, a number of instances of unchanging values have been described in starvation and even a significant increase has been reported for a malnourished child, which has been related to either pure protein-malnutrition or potential differences in metabolism between non-adults and adults (Neuberger et al. 2013). Thus, the possibility that higher $\Delta^{13}C$ shifts among Moro de Alins non-survivors may coincide with isotopic effects of physiological stress cannot be dismissed.

In any case, individuals younger than 2 years usually have a high rate of infectious disease that adversely affects their health and nutritional status (Rowland et al. 1988). Although there can be contributions from respiratory illnesses, diarrhea seems to be particularly important in mortality and morbidity, perhaps because of its association with malabsorption of nutrients, as well as anorexia and catabolism (Mata 1992). In prehistoric contexts such as Moro de Alins, drinking and cooking water may have been especially prone to contamination. It is well known that commonly used transport and storage containers are easily contaminated with human and/or animal fecal matter or urine containing pathogens, particularly when there were open defecation areas, corrals, intensive grazing, abandoned dug wells, or garbage pits close to wells or water storage vessels, or uphill from freshwater sources. Even if this were not the case, the

use of wide-mouth containers to store water, particularly if uncovered, would allow hands, cups/ladles, and insect and animal vectors to come into contact with the water. In addition, the location of containers on the floor or ground would allow easy access to water by children and animals, which may have been common sources of water contamination (UNICEF 2008) and, therefore, of diarrhea and other water-borne diseases. Physiological stress associated to these diseases may have also played a role in the larger $\Delta^{15}$N trophic shifts detected among both survivors and non-survivors in Moro de Alins.

## Isotopic insights into the post-weaning period

In contrast to the weaning period, a number of instances of opposing covariance have been identified in the post-weaning period, suggesting the existence of episodes of physiological stress, in some cases preceding death in childhood (MOR2, MOR4, and MOR10). There are also some possible dietary explanations for a rise in $\delta^{15}$N values without a corresponding rise in $\delta^{13}$C, such as the consumption of freshwater fish or meat from animals raised in heavily forested environments (both often showing comparatively low $\delta^{13}$C values) (Drucker et al. 2008; Dufour et al. 1999). However, these subsistence practices have not been documented among northern Iberian late prehistoric communities, and the fact that $\delta^{15}$N values in most children rise just prior to death is more plausibly explained by physiological stress. In modern populations, it has been found that non-breastfed younger children have a higher risk of diarrheal illness, a longer mean duration of illness, and a 3.5 times higher risk of death, compared to breastfed children (Mølbak et al. 1994). This is essentially because the former lack the immunological support of breastmilk (Briend et al. 1988; Briend and Bari 1989) and their own immune systems are not yet fully developed (Burgio et al. 1980). Also, the nutritional support of breastmilk beyond age 2 may be crucial for survival in deprived, pre-vaccination, and/or pre-antibiotic settings. The word *kwashiorkor* from the Ga language of Accra, Ghana, which designates a severe protein (and/or calorie) deficiency and means "the disease of the deposed child," exemplifies well the importance of supplementary breastmilk between 2–4 years, when disease risk is high, in contexts where children's diets are almost exclusively cereal-based and sanitation is poor (Williams et al. 1935). Far from suggesting such a hostile context, our data may support a key role of the cessation of breastfeeding in early childhood morbidity and mortality in Moro de Alins and perhaps, indirectly, the potential impact that the birth of a new child may have had on the diet and health of an older child, if that was a cause of weaning cessation.

Other post-weaning isotope instances compatible with catabolic changes, particularly those detected along the isotope sequences of the individuals who survived childhood (e.g., MOR3 from age 8.5 to 9.5 years; MOR7 around age 4, age 5 to 6, and, possibly, around age 7 years; and MOR11 from age 5 to 6 years) suggest that they may also have experienced intermittent stress episodes, as supported by the presence of a number of instances of linear enamel hypoplasia occurring in early childhood (Alconchel 2017). Despite the presence of linear enamel hypoplasia traditionally being related to so-called weaning stress (for a review, see Katzenberg et al. 1996), there is clear evidence that the peak ages of occurrence tend to happen in a number of late prehistoric contexts across Europe during the immediate post-weaning period (e.g., Cucina 2002; Tomczyk et al. 2012). This offers support for the post-weaning period being potentially as or more stressful—particularly from age 3 to 5 years–than weaning. This situation is designated in this paper as the "post-weanling's conundrum." Children's naïve immune responses and increased motor and language capabilities, which expose them to frequent contact with more individuals and more substances, have been described as key factors that increase the chance of disease transmission in the post-weaning period (e.g., Blakey et al. 1994). Children's increasing contributions to domestic tasks and subsistence and/or technological activities may have been an additional source of stress from age 4–6 years onwards (Derricourt 2018).

In this regard, it is particularly interesting to mention the Iberian Bronze Age site of La Motilla de Azuer, a fortified enclosure formed by concentric walls with a central tower and open-air well surrounded by a small settlement and a necropolis, located in the Meseta region (Nájera et al. 2010). There, 41% of individuals (19 out of 46) show evidence of linear enamel hypoplasia between 0.5 and 7 years of age, with a concentration of occurrences between 2.5 and 4.5 years and a clear peak at age 3–3.5 years, while the cessation of weaning was isotopically estimated to be at age 2.5 years (Nájera et al. 2010). Moreover, 50% of children had skeletal evidence of growth disruption (detected through discrepancies between dental and long bone age estimates), and there is musculo-skeletal evidence of child labor from the age of 7 years onwards (Nájera et al. 2010). Additionally, many children exhibit high bone collagen $\delta^{15}$N values attributed to physiological stress after the weaning process (Nájera et al. 2010). Other Bronze Age sites from southeast Iberia have also briefly reported bone collagen isotope evidence of physiological stress or nutritional deficiencies among weaned infants and younger children (Knipper et al. 2020; Molina et al. 2019).

There are no other isotopic studies of incremental tissues of Iberian Bronze Age populations apart from the one presented here, and very few in a wider European context have paid particular attention to physiological effects resulting from the cessation of breastfeeding. The consistently lower

dentine mean $\delta^{13}C$ and $\delta^{15}N$ values shown by individuals surviving into adolescence or adulthood at Moro de Alins may tentatively suggest that fewer catabolic processes (cf. Neuberger et al. 2013) occurred in their early lives, from which we can infer lower exposure to stress and/or improved metabolic resilience. Balanced high-quality diets, including both plant (such as cereals, legumes, vegetables, nuts, fruits, tubers, and fungi) and animal sources (dairy products and meat primarily from domesticates), adequate sanitary conditions, particularly access to safe drinking and cooking water and hand hygiene, and social contact limited to a small group, have been documented to be highly important for young children's health and survival (e.g., Blakey et al. 1994; Iannotti 2018; UNICEF 2008), as possibly was the case for some or even many of the Moro de Alins children. These findings evoke ideas of life history theory and the developmental origins of health and disease paradigm in suggesting variation in adaptive plasticity at each life stage and also in proposing early life nutritional conditions as key to mitigate or exacerbate the expression of life-history trade-offs on health and survival at later stages of life (McDade 2003; Temple 2019).

## Conclusion

Incremental isotopic analysis of primary dentine can provide a reconstruction of aspects—both dietary and physiological—of the early life of an individual that allow for an exploration of the relationship between early life environments, particularly those involving the mother-infant nexus, and risks for disease and mortality later in life. Sequential dentine $\delta^{15}N$ and $\delta^{13}C$ data of Bronze Age individuals from Moro de Alins in north-eastern Iberia show values compatible with generally short exclusive breast-feeding ($0.3 \pm 0.2$ years) and medium-length weaning periods ($2.3 \pm 0.7$ years). The results show differences in $\Delta^{13}C$ trophic shifts (between exclusive breastfeeding and immediate post-weaning periods) between individuals who survived into adolescence or adulthood and those who did not, with the former exhibiting shifts that are more consistent with most modern mother-infant pairs published. This outcome suggests that those individuals who consumed more (isotopically) similar foods to their mothers, or suffered from less physiological stress during the weaning process and beyond, had greater chances of survival. Moreover, a number of isotopic instances suggestive of episodes of physiological stress mainly occurred in the post-weaning period. The loss of the nutritional and antimicrobial support of breastmilk while younger children's immune systems were still immature, and dietary needs and exposure to pathogens were increasing, may have made this period the most perilous in juvenility. We have designated this situation as the "post-weanling's conundrum." Our results support the key role of nutritional

status in early morbidity and mortality among partially and especially fully weaned children of pre-antibiotic, pre-vaccination, and potentially poor sanitation settings and suggest that health and survival in adults are rooted in early life experiences.

## Declarations

**Conflict of interest** The authors declare no competing interests.

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