Short title: Famine and stable isotope analysis

Running title: Assessment of nutritional stress in famine burials using stable isotope analysis

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Abstract:

Objectives

We compared $\delta^{15}N$ and $\delta^{13}C$ values from bone and dentine collagen profiles of individuals interred in famine-related and attritional burials to evaluate whether individuals in medieval London who experienced nutritional stress exhibit enriched nitrogen in bone and tooth tissue. Dentine profiles were evaluated to identify patterns that may be indicative of famine during childhood and were compared to age of enamel hypoplasia (EH) formation to assess whether isotopic patterns of undernutrition coincide with the timing of physiological stress.

Materials and Methods

$\delta^{15}N$ and $\delta^{13}C$ isotope ratios of bone collagen were obtained from individuals (n=128) interred in attritional and famine burials from a medieval London cemetery (c. 1120–1539). Temporal sequences of $\delta^{15}N$ and $\delta^{13}C$ isotope profiles for incrementally forming dentine collagen were obtained from a subset of these individuals (n=21).

Results

Results indicate that individuals from attritional graves exhibit significantly higher $\delta^{15}N$ values but no significant differences were found between burial types for the sexes. Analyses of dentine profiles reveal that a lower proportion of famine burials exhibit stable dentine profiles and that several exhibit a pattern of opposing covariance between $\delta^{15}N$ and $\delta^{13}C$. EH were also observed to have formed during or after the opposing covariance pattern for some individuals.

Conclusions

The results of this study may reflect differences in diet between burial types rather than nutritional stress. Though nutritional stress could not be definitively identified using bone and dentine collagen, the results from dentine analysis support previous observations of biochemical patterns associated with nutritional stress during childhood.

1. Introduction

During the Late Medieval Period (c. 12th–16th centuries), excessive rains and flooding across Europe caused recurring poor harvests (Farr, 1846; Scrimshaw, Taylor, & Gordon, 1968). This resulted in food shortages across Europe and several instances of famine throughout the period (Keys, Brožek, Henschel, Michelsen, & Taylor, 1950; Rawcliffe, 2013), most notably the Great Famine (1315–1317) that killed 10–15% of the population in England (Jordan, 1997). In London, the effects of famine were likely compounded by intensive urbanization during the medieval period; for example, the population of London almost quadrupled from the 12th century to the beginning of the 14th century (Schofield, 2011; Williams, 1963).

Londoners, unlike their rural counterparts, did not generally produce their own food, making them dependent on the market and surrounding rural areas for food supplies (Galloway & Murphy, 1991). During periods of famine, high food prices and declining wages for occupational specialists unable to sell their goods reduced the ability of urban residents to purchase food (Jordan, 1997; Wrigley, 1969). Because of this, famine had the greatest impact on the poor, particularly those in crowded urban settings where food was in short supply and disease spread easily (Walter & Schofield, 1985).

Mortality crises often result from outbreaks of infectious disease associated with severe food shortages, suggesting that an insufficient diet would have caused greater susceptibility to infection during this period (Duncan, Scott, & Duncan, 1993; Dyson, 1991; Galloway, 1985; Galloway, 1988; Mielke, Jorde, Trapp, Anderton, Pitkanen, & Eriksson 1984). Excess mortality that correlates with incidences of famine is evident in the archaeological record in the form of catastrophic mass burials in London (Connell, Jones, Redfern, & Walker,

2012). The existence of these famine burials, and their use for examining the association between famine and mortality (e.g., DeWitte & Yaussy, 2019; Yaussy, DeWitte, & Redfern, 2016), raises the possibility of investigating isotopic signatures of famine in skeletal remains and assessing the association between tissue stable isotope ratios and proxies of poor health.

Several bioarchaeological studies of cemetery collections in medieval England have investigated the detrimental health effects of undernutrition (see, among others, Brickley & Ives, 2010; DeWitte & Yaussy, 2017; Mays, Brickley, & Ives, 2006; Roberts, 2009; Roberts & Cox, 2003). Undernutrition is the insufficient provision of energy and nutrients to meet the requirements of the body to maintain good health and is a condition that can cause a stress response in the body (De Onis, Monteiro, Akré, & Glugston, 1993), referred to here as "nutritional stress". The assessment of nutritional stress using skeletal indicators (e.g., cribra orbitalia) is problematic, as many can be produced by various etiologies. Moreover, individuals who were more frail (i.e., with a higher risk of death) than their peers may have died relatively quickly, not surviving long enough for skeletal markers of nutritional stress to form (Wood, Milner, Harpending, & Weiss, 1992); thus, frailer individuals who died from famine may not exhibit skeletal lesions characteristic of nutritional stress macroscopically on their bones.

Stable isotope data from bone and tooth samples can contribute to our understanding of nutritional stress and health. Specifically, stable isotope analysis may be informative about how $\delta^{13}C$ and $\delta^{15}N$ values are manifested among individuals who experienced nutritional stress. Further, the analysis of isotope data from teeth (forming early in life) and bone (forming prior to death) together can provide a more nuanced understanding of diet and health across the life course (Reitsema & Vercellotti, 2012).

Clinical (Fuller, Fuller, Sage, Harris, O'Connell, & Hedges, 2004, 2005; Mekota, Grupe, Ufer, & Cuntz, 2006, 2009), bioarchaeological (Beaumont, Geber, Powers, Wilson, Lee-Thorp, & Montgomery, 2013a; Beaumont, Gledhill, Lee-Thorp, & Montgomery, 2013b; Beaumont & Montgomery, 2016; Eerkens, Hull, Goodman, Evoy, Kapp, Hussain, & Green, 2017; Holder, Dupras, Jankauskas, Williams, & Schultz, 2017; Olsen, White, Longstaffe, von Heyking, McGlynn, Grupe, & Rühli, 2014; Redfern, DeWitte, Beaumont, Millard, & Hamlin, 2019; Reitsema, 2013), and forensic (Baković, Vreča, & Mayer, 2016; Neuberger, Jopp, Graw, Püschel, & Grupe, 2013) research show that enriched $\delta^{15}N$ may be indicative of nutritional stress or starvation. Under metabolic stress, enriched $\delta^{15}N$ results from insufficient new nitrogen consumption, causing the body to enter a catabolic state (Hobson, Alisauskas, & Clark, 1993). Prolonged protein deprivation causes changes in the body's metabolic production and breakdown of protein in lean tissues, causing the preferential routing of ^{14}N via catabolism to liberate amino acids for the maintenance of other bodily functions and resulting in ^{15}N enrichment (Orten & Neuhaus, 1982). For example, a clinical study tracking dietary changes in isotopic ratios revealed that in patients suffering from anorexia nervosa, $\delta^{15}N$ was highest when BMI levels were low (Mekota et al., 2006). These and other findings suggest that individuals interred during periods of famine, and thus likely facing and perhaps succumbing to nutritional stress, would exhibit elevated $\delta^{15}N$ values compared to individuals interred during non-famine periods. This would potentially allow bioarchaeologists to identify biochemical markers of famine in human remains.

Further, using modern hair samples, Neuberger et al. (2013) found that during starvation, $\delta^{13}C$ values generally decrease concurrently with increasing $\delta^{15}N$ values. The authors

suggest that because body fat is already depleted in ^{13}C unlike other tissues like muscle, a body experiencing nutritional stress will recycle carbon from fat deposits, integrating more ^{12}C into the newly synthesized tissues, resulting in lower $\delta^{13}C$ values. Thus, like nitrogen, nutritional carbon isotope ratios can also be informative about the breakdown of body fat deposits in starving individuals (Neuberger et al., 2013). It can also be useful for assessing changes in consumption practices influenced by limited access to food (Beaumont & Montgomery, 2016).

1.1 Aims and Objectives

To evaluate whether individuals who experienced nutritional stress in medieval London exhibit ^{15}N-enriched tissues, this study compared $\delta^{15}N$ values from bone collagen of individuals interred in famine mass burials and individuals interred in attritional burials (who were less likely to have experienced nutritional stress) from the St Mary Spital cemetery (SRP98) in medieval London (c. 1120–1539).

Previous research on skeletal assemblages has not yet revealed a definitive association between elevated $\delta^{15}N$ values and famine using bone collagen because of slow bone turnover rates (Beaumont et al., 2013a; Beaumont & Montgomery, 2016). Given, however, that London experienced several instances of famine during the Late Medieval Period (Rawcliffe, 2013) rather than a single catastrophic famine event and that most of those buried in SRP98 were poor (individuals disproportionately affected by famine), it may be possible to detect elevated $\delta^{15}N$ values resulting from nutritional stress in this assemblage. We hypothesized that individuals in famine burials would exhibit ^{15}N-enriched tissues, and thus elevated $\delta^{15}N$ values compared to individuals in attritional burials. We also expected $\delta^{13}C$ values to be reduced for

individuals in famine burials due to the breakdown of body fat deposits during nutritional stress. Additionally, $\delta^{15}N$ and $\delta^{13}C$ were compared separately for the sexes to evaluate whether famine affected the sexes differently. Given that famine was experienced by both sexes in London, we hypothesized that males and females would both exhibit elevated $\delta^{15}N$ values when analyzed separately.

Incremental dentine collagen analysis was conducted on a subset of individuals to evaluate longitudinal patterns of variation in isotope ratios during childhood and adolescence to identify possible indicators of nutritional stress in famine burials. Because dentine profiles provide a better resolution of the timing of changes in stable isotope values, we hypothesized that individuals interred in famine burials will exhibit periods of increasing $\delta^{15}N$ values and decreasing $\delta^{13}C$ values (opposing covariance) throughout childhood (after weaning age) as they experienced nutritional stress. Finally, to assess whether isotopic patterns of undernutrition coincide with physiological stress, the approximate ages of enamel hypoplasia (EH) formation for these individuals, where present, were compared to their incremental dentine collagen profiles. We hypothesized that the age at which an EH forms would coincide with an increase in $\delta^{15}N$ values and concurrent decrease in $\delta^{13}C$ values.

2 Materials and methods

To evaluate potential biochemical markers of famine, bone collagen $\delta^{13}C$ and $\delta^{15}N$ ratios were compared between individuals within attritional interments (n=71) and within famine interments (n=57). To evaluate differences between the sexes, males (n=58) and females (n=53) were analyzed separately. The Mann-Whitney U test, a non-parametric test for pairwise

comparison, was used, as this test does not require an assumption of normality. For both grave types, dentine collagen $\delta^{13}C$ and $\delta^{15}N$ values (bulk and incremental) were compared to $\delta^{13}C$ and $\delta^{15}N$ bone collagen values to assess isotopic change and potential nutritional stress (e.g., an increase in nitrogen values) throughout life. Incremental dentine collagen profiles for each individual were also compared to age of EH formation, if present, to assess whether fluctuations in isotope values coincide with physiological stress (i.e., delayed enamel mineralization).

2.1 St Mary Spital cemetery

The St Mary Spital cemetery skeletal collection is a large, well-dated skeletal assemblage curated by the Museum of London. The cemetery was used (c. 1120–1539) during a time of intensive urbanization in medieval London and when the city experienced several famines (Connell et al., 2012). The cemetery was used by the general community, but also includes burials of inmates from the associated infirmary, officials, and benefactors of the hospital, and contains individuals of all ages (Connell et al., 2012); given that the individuals interred in the cemetery are drawn "from across London and the wider region" (Connell et al., 2012: p.14), the cemetery is likely biased toward lower status individuals who made up the bulk of the English population at this time. An approximately equal number of individuals were sampled from each temporal period in SRP98 (see Table 1). The temporal periods of use in the cemetery were determined via high-precision Bayesian radiocarbon dating within a well-defined stratigraphic framework (see Sidell, Thomas, & Bayliss (2007) for details regarding phasing of the cemetery

using Bayesian modelling). The temporal periods include: Period 14 (c. 1120–1200), Period 15 (c. 1200–1250), Period 16 (c. 1250–1400), and Period 17 (c. 1400–1539).

Within SRP98, different burial types are associated with periods of attritional mortality patterns (type A: single body in a grave, type B: 2–7 bodies horizontally interred in a single grave, or type C: 2–11 bodies stacked in a single grave) and crisis mortality patterns (burial type D: 8–45 bodies in a single grave) (Connell et al., 2012). Differences in demographic patterns between the burial types and the correlation of these burials with documented years of famine indicate that type D burials are the result of famine-related crises. For Period 16, however, it is possible that the mass burials are associated with the 14th-century Black Death epidemic rather than famine, so our analyses do not include this period and will thus provide a relatively conservative assessment of potential differences in isotope values between burial types. Though trends in some skeletal pathologies might indicate that the attritional burials contain higher proportions of infirmary inmates compared to the mass burials (e.g., Connell et al., 2012: p. 156), there is no independent information about the precise composition (by inmate status or socioeconomic status) of the various burial types.

2.2 Skeletal and tooth analysis

Sex was estimated for each individual using sexually dimorphic features of the pelvis and skull (Buikstra & Ubelaker, 1994; Phenice, 1969). Epiphyseal closure and dental development were used to differentiate nonadults from adults per Cunningham, Scheuer, and Black (2016) and Al Qahtani, Hector, and Liversidge (2010), respectively. Individuals with an estimated age-at-death of 15 years or older are classified as adults, and those below 15 years of age are

classified as nonadults (n=12) and were not included in sex-specific analyses. Adult age-at-death was estimated using transition analysis (Boldsen, Milner, Konigsberg, & Wood, 2002) via the ADBOU (Anthropological Database, Odense University) age estimation software with an informative prior distribution of age-at-death (the Gompertz-Makeham model, see Wood, Holman, O'Connor, & Ferrell, 2002) estimated from 17th-century Danish rural parish records.

The presence of and age at which EHs formed (Reid & Dean, 2000) were included in the analysis of dentine profiles. EH is a dental enamel defect caused by disruptions in the metabolism of enamel-forming cells that can occur as a result of physiological stress (Huss-Ashmore, Goodman, & Armelagos, 1982). EHs can manifest as linear defects or as defined pits around, or partially around, the enamel surface during tooth development, and have been found to be a good indicator of physiological stress during childhood (Goodman, 1991). Though EH may have a multifactorial origin (Neiburger, 1990), it is still used here, with caution, because it is the only potential skeletal indicator of stress that can be assigned an age-at-development and can concurrently form with the dentine measured for stable isotope ratios. Only the maxillary and mandibular permanent canines were assessed for presence of EH, as this tooth type is highly sensitive to physiological stress (Huss-Ashmore et al., 1982).

2.3 Sampling for isotope analysis

Bone samples were obtained from ribs with no evidence of pathological bone formation. The samples were prepared using a modified Longin method (Brown, Nelson, Vogel, & Southon, 1988) at the University of Bradford Stable Light Isotope Laboratory (UBSLI) and were measured in duplicate and compared with UBSLI and international standards (see

Supplemental Materials for collagen preparation and analysis protocols and standards used by UBSLI). Collagen quality was determined following Van Klinken (1999), DeNiro (1985), and Ambrose (1990), and resulted in the exclusion of three samples (see Supplemental Materials for specific samples and collagen quality data). Isotope values of bone collagen from Lakin's (2010) isotopic analysis of SRP98 were included (n=13; samples are specified in Supplemental Materials) and follow the same sample collagen quality requirements. There are no correlations between any of the collagen preservation indicators (e.g., collagen yield, atomic C:N, %N, and %C) for the samples used in this study, indicating that there is minimal diagenetic alteration of the stable isotope signatures (Ambrose, 1990). The results are expressed using the delta (δ) notation in parts per thousand (per mil or ‰). The instrument measurement standard deviation from runs of standards is ±0.19 (1 SD) for nitrogen and ±0.10 (1 SD) for carbon.

2.3.2 Tooth samples

In addition to comparison of $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen from attritional and famine burial types, incremental dentine analysis of carbon and nitrogen isotopes was conducted for tooth samples from individuals who were also sampled for bone collagen (attritional n=10, famine n=11, see Table 1). This subset of individuals was randomly sampled from the overall study sample of individuals sampled for bone collagen. In contrast to bone, primary dentine does not remodel and can provide a time-bound archive of isotopes during tooth formation (Beaumont et al., 2013a). Because the rate of human tooth development is well established (Hillson, 2005), age intervals may be attributed to incremental samples with a single tooth, producing a high-resolution record of isotopic changes during childhood with

some averaging due to the orientation of the dentine layers; however, dentine collagen cannot provide isotopic data from the period just prior to death unless the individual died during childhood or adolescence while the tooth was still forming. Incremental dentine may be useful for identifying dietary patterns or nutritional stress during childhood that could have affected an individual's risk of death during famine.

For this study, first and second molars and premolars were sampled (see Table 2 for approximate years of tooth mineralization). Samples were obtained from teeth with minor tooth wear and no pathological conditions. Teeth were sectioned and prepared per Beaumont and Montgomery (2015) Method 2 (see Supplemental Materials for details regarding this process). Each tooth section was assigned an approximate age by averaging the number of sections with the total mineralization span of the tooth; $\delta^{15}N$ and $\delta^{13}C$ values from each section were then assigned to that approximate age. Dentine collagen samples were prepared and preservation was determined using the same standards applied to the bone collagen samples. The results are expressed using the delta (δ) notation in parts per thousand (per mil or ‰). The instrument measurement standard deviation from runs of standards was determined is ±0.19 (1 SD) for nitrogen and ±0.10 (1 SD) for carbon.

3 Results

3.1 Bone sample results

Carbon and nitrogen stable isotope values for bone collagen are provided in the Supplemental Materials. $\delta^{13}C$ and $\delta^{15}N$ are plotted by burial type in Figure 1 and summarized with sample sizes in Table 3. Analyses comparing bone collagen isotope values between

attritional and famine burials reveal that individuals interred in attritional graves exhibit higher $\delta^{15}N$ values compared to individuals in famine graves (Table 4 and depicted in Figure 2). Weaning is unlikely to have affected the stable isotope values for bone collagen. Given that bone remodels rapidly during early childhood (Valentin, 2002) and weaning is generally complete by approximately 2–3 years in medieval England (Haydock, Clarke, Craig-Atkins, Howcroft, & Buckberry, 2013; Richards, Mays, & Fuller, 2002), it is unlikely that weaning largely affected the values of the two youngest individuals in the sample who were at least 5 years of age at death. Furthermore, the results of the famine and attritional burial comparison are similar when all nonadults are excluded (Table 4).

These results are contrary to what was hypothesized, i.e., that the famine burials would exhibit higher $\delta^{15}N$ values because of physiological responses to nutritional stress. Rather than reflecting nutritional stress during famine, this difference could actually be capturing dietary differences between the burial types due to exposure to famine (i.e., more high-trophic-level protein consumed by individuals in attritional burials). Additionally, the median for $\delta^{13}C$ values is consistently lower in the attritional burials, though this difference is not significant; this is to be expected, as $\delta^{13}C$ values are generally less variable than $\delta^{15}N$ values except in individuals shifting, for example, between a C_3- and C_4-based diet. Additionally, the famine burial isotope values have a slightly higher standard deviation ($\delta^{15}N$ σ=1.1, $\delta^{13}C$ σ=0.5) than the attritional burials ($\delta^{15}N$ σ=1.0, $\delta^{13}C$ σ=0.4). Though the difference is small for both $\delta^{15}N$ and $\delta^{13}C$, it may be reflective of slightly more dietary variability in the famine burials, as individuals adapted to limited accessibility to food supplies during famine.

Isotope values of bone collagen for the sexes are plotted by burial type in Figure 3 and summarized with sample sizes in Table 3. Sex-specific pairwise comparisons of isotope values between burial types are shown in Table 4. Females in attritional burials exhibit elevated $\delta^{15}N$ values, though the difference is not significant at $\alpha=0.05$ ($p=0.09$), and there is no difference in $\delta^{13}C$. For males, there are no significant differences in $\delta^{13}C$ or $\delta^{15}N$ between the burial types.

3.2 Incremental dentine results

The results of the incremental dentine analysis for each tooth are provided in the Supplemental Materials. Contrary to what was hypothesized, individuals in famine burials did not exhibit increasing $\delta^{15}N$ throughout childhood. However, a higher proportion of individuals in famine burials exhibit fluctuations in $\delta^{15}N$ values (at least ≈2‰ increase or decrease in isotope values of dentine collagen sections across the profile) after three years of age (i.e., after weaning) compared to attritional burials, and these are of shorter duration (famine=7/11, attritional=3/10). Most of the fluctuations observed in the attritional burials occurred over several years (two of the three individuals), likely to reflect true dietary changes, while only two of the seven individuals in famine burials exhibit gradual fluctuations. $\delta^{13}C$ values generally do not vary much, staying within a range of -20.1‰ to -18.2‰. We have focused on dentine profiles after three years of age because weaning was generally complete by 2–3 years of age in medieval England (Haydock et al., 2013; Richards et al. 2002).

3.2.1 Potential markers of famine

The lower proportion of famine burials exhibiting a stable dentine profile during childhood compared to attritional burials is consistent with the overall slightly higher variability of isotope values seen in the famine burials for bulk bone collagen samples, and is suggestive of a stable diet during childhood for individuals in attritional burials. All except two of these individuals have bulk bone collagen $\delta^{15}N$ values generally reflecting diet for at least the last 10 years of life that are within 1‰ of the oldest dentine $\delta^{15}N$ value (≈9.5–14.5 years of age), suggesting that the (isotopically) stable diet seen in childhood likely continued into adulthood. The fluctuating dentine profiles observed in famine burials may be a reflective of a physiological response to undernutrition (i.e., tissue catabolism) or a wider variation in available food sources.

Additionally, a pattern in $\delta^{15}N$ and $\delta^{13}C$ values that has been associated with nutritional stress in other studies was also observed here, and, in some cases, occurred concurrently with EH formation. Where there is a dietary trophic-level shift, we expect to see that both $\delta^{15}N$ and $\delta^{13}C$ values rise. As described above, tissue catabolism causes ^{15}N enrichment in tissues that results in elevated $\delta^{15}N$ values. In addition to this, when fewer carbohydrates are consumed, as is typical during periods of undernutrition, the $\delta^{13}C$ level in the body is not maintained due to breakdown of body fat deposits, resulting in reduced $\delta^{13}C$ values. Together, this creates a pattern of increasing $\delta^{15}N$ as $\delta^{13}C$ decreases. Mekota et al. (2006) found this pattern in hair samples of anorexia patients, with $\delta^{15}N$ values increasing as both $\delta^{13}C$ values and BMI decreased. When the patients began to recover and BMI levels increased, the $\delta^{15}N$ values decreased and $\delta^{13}C$ values increased. Eerkens et al. (2017) also found this pattern in a series of hair samples from a girl believed to have died as a result of nutritional stress. Beaumont and

Montgomery (2016) reported this pattern in dentine profiles of individuals during the Great Irish Famine, which they describe as "opposing covariance," and also suggest that a lack of change in $\delta^{13}C$ while $\delta^{15}N$ increases could still be construed as potential nutritional stress rather than a trophic-level shift. More recently, this was pattern was also observed in incremental dentine of children from a British Anglo-Saxon population and was attributed to possible nutrition stress (Beaumont, Craig-Atkins, Buckberry, Haydock, Horne, Howcroft, Mackenzie, & Montgomery, 2018). SRP98-30920 (Figure 4, top) from a famine burial has a dentine profile that exhibits the opposing covariance pattern at ages ≈3–7 years; SRP98-10765 (Figure 4, bottom) from an attritional burial, however, exhibits a dentine profile with concurrent increases and decreases in $\delta^{15}N$ and $\delta^{13}C$ throughout childhood (≈3.5–14.5 years), which is more typical of trophic-level dietary change.

Five of the eleven individuals from famine burials sampled for incremental dentine analysis distinctly exhibit the opposing covariance pattern. SRP98-30920 exhibits the opposing covariance pattern at ≈3–7 years and an EH formed at 3.6 years just as the opposing covariance pattern is beginning (Figure 5). Given that EHs indicate the experience of some form of physiological stress during mineralization (Hillson & Bond, 1997) and that this individual exhibits patterns of opposing covariance during formation, this suggests that the isotope values are more likely reflecting nutritional stress rather than dietary change. An adult male (SRP98-20682) also exhibits opposing covariance during childhood (Figure 6). At ≈2.5–3 years of age there is a decrease in $\delta^{15}N$ (-2.8‰) and increase in $\delta^{13}C$ (+0.2‰) that could be associated with weaning. $\delta^{15}N$ and $\delta^{13}C$ then exhibit opposing covariance from ≈4.5–8 years. An EH was identified on the enamel of the permanent canine at approximately 4.8 years, which is at the

beginning of the opposing covariance pattern and when there is a rapid increase of ≈2‰ in $\delta^{15}N$ within months. Because the canine mineralizes by 6 years of age, it is not possible to know if physiological stress was experienced for the duration of the opposing covariance pattern. The bone collagen isotope values of this individual indicate that the final increase in isotope ratios remained into adulthood and is within the average for the cemetery bone collagen values.

Not all individuals have EHs forming concurrently with opposing covariance; however, this may be because of the age at which the canine mineralizes (1.5–6.2 years) does not completely overlap with the mineralization ages for the sampled tooth or because nutritional stress was not severe enough to affect tooth mineralization (Neiburger, 1990). SRP98-9632, a young adult male from a famine grave, exhibits the opposing covariance pattern from approximately 6 to 8 years (Figure 7, top). Additionally, SRP98-9789, an adult male from a famine grave, exhibits the opposing covariance pattern at ≈11 years until the sampled tooth completes formation at 13.5 years (Figure 7, bottom). For both of these individuals, the canine has completed mineralization prior to the opposing covariance pattern and thus it is not possible to associate physiological stress to these periods of possible undernutrition. Similarly, SRP98-32302 exhibits opposing covariance at ≈3.5–6 years (Figure 8), which is after weaning age; two EHs are observed, however, both formed prior to the mineralization of the sampled tooth (2.7 and 3.1 years) and thus cannot be compared to the dentine profile.

Moreover, this pattern is also observed in two of the ten individuals sampled for dentine analysis from the attritional burials, suggesting that it is not unique only to famine burials. The opposing covariance pattern for these individuals, however, is not as distinct, with a smaller

range of $\delta^{15}N$ fluctuations (within 1‰) (SRP98-21273) or opposing covariance between $\delta^{15}N$ and $\delta^{13}C$ occurring over several years (SRP98-5287).

4 Discussion

4.1 Bone collagen samples and burial type

Rather than reflecting differences in nutritional stress experienced between burial types, these results may reflect true differences in dietary sources that occurred as a consequence of famine. That is, individuals in attritional burials may have been eating different proportions or types of foods compared to individuals in the famine burials. The high $\delta^{15}N$ values and the matching $\delta^{13}C$ values in the attritional burials suggests more high-trophic-level protein in the diet such as freshwater fish and/or animal meat than the diet of individuals in famine burials.

Unfortunately, there is a dearth of literature regarding what specific foods may have been consumed in England during periods of famine or what kind of opportunistic foods would have been available, as historical records regarding the medieval English diet tend to focus on the time period as whole. It is well-established that grain was medieval England's primary food source (Dyer, 2002) and that famine is generally attributed to the reduced availability of grain (Farr 1846). It has been documented, however, that those affected by famine consumed poor quality food, such as old bread or rancid meats, due to the substantial price increase in decent quality foods (Goldberg, 2004). Differences in food quality, however, cannot be assessed through stable isotope analysis, as the quality of food does not affect the stable isotopic signature. Animals would also have been affected by famine conditions and thus were likely to

be less available to the affected poor. Rawcliffe (2013) notes that individuals in London during non-famine periods would have had better access to high-trophic-level foods, such as fish and terrestrial animal proteins, compared to individuals experiencing famine, which is consistent with the higher $\delta^{15}N$ values of individuals interred in attritional burials in this sample (Pearson, Levey, Greenberg, & Del Rio, 2003; Sponheimer, Robinson, Ayliffe, Roeder, Hammer, Passey, … Ehleringer, 2003a; Sponheimer, Robinson, Roeder, Passey, Ayliffe, Cerling, … Ehleringer, 2003b).

Interestingly, the difference in $\delta^{15}N$ values between burial types in this study is similar to that observed by Müldner, Montgomery, Cook, Ellam, Gledhill, and Lowe (2009) between high- and low-status individuals at Whitehorn Cathedral in 13–14th-century Scotland. They observe higher $\delta^{15}N$ values in high-status individuals and attribute this difference to better access to fish, suggesting that the lack of a marine signature in general may be indicative of a low-status diet. Dyer (1989) notes through analysis of historical records that in medieval England, high-status individuals consumed more animal meat and fish compared to the poor.

The difference between attritional and famine burials observed in this study could be analogous to the observed isotope patterns and documented consumption differences between high- and low-status individuals. Perhaps, during famine, individuals were not able to supplement their cereal-based diet with fish and/or animal meat, using whatever funds they had for the cheapest sources available, mimicking a low-status diet. Additionally, marine foods, particularly salted fish, were generally accessible in London's large market (Woolgar, 2000). It would not be surprising that an unstable market during famine (Sen, 1981) could have resulted in reduced access to these high-tropic-level protein sources. As discussed above, SRP98 was mostly comprised of the poor and so it is unlikely that the small proportion of high-status

individuals included in the cemetery would affect the results even if they were exclusively in attritional burials.

Additionally, Curto, Mahoney, Maurer, Barrocas-Dias, Fernandes, and Fahy (2019) found that individuals with non-specific generalized infections exhibited reduced $\delta^{15}N$ values compared to those without lesions and those with only healed tibial periostitis. The authors argue that the individuals who exhibited signs of generalized infection at death likely consumed a diet lower in terrestrial animal protein, increasing their susceptibility to pathogens that led more frequently to generalized infections. This is consistent with the findings from numerous studies in humans and animal models that protein malnutrition influences the immune system (Caler 2013; Li, Yin, li, Kim, & Wu, 2007; Losada-Barragán, Umaña-Pérez, Cuervo-Escobar, Berbert, Porrozzi, Morgado, … Cuervo, 2017). Thus, the lower proportion of protein consumed by individuals facing famine in this study could have increased their susceptibility to infection and eventually death.

Rather than differences in diet, it is also possible that the consumption of protein from lower trophic levels by those experiencing famine could have obscured an increase in $\delta^{15}N$ values resulting from tissue catabolism, which in turn was produced by nutritional stress. That is, during famine, individuals may have consumed a low proportion of protein or lower-trophic-level protein and this may have cancelled out ^{15}N enrichment occurring during catabolism as it was averaged into the bone tissue. This reasoning may also be why Beaumont et al. (2013a) did not observe elevated $\delta^{15}N$ values of Great Irish Famine victims, as these individuals who were experiencing undernutrition were also eating low trophic-level foods.

Though we expected that the occurrence of multiple famines during this period in London would have made it possible to observe nutritional stress isotopically in this sample, the results show that identifying nutritional stress using bone collagen alone is limited by slow tissue turnover rates. Hedges, Clement, Thomas, and O'Connell (2007) argue that isotopic values derived from human bone collagen may reflect the average adult diet for the last 20–30 years before death, rather than the estimate of 4–10 years by Valentin (2002). Bone turnover rates also generally decrease with age (Hedges et al., 2007; Klepinger, 1984), making it difficult to estimate the timespan that the isotope values actually reflect. Unless chronically affected by famine throughout life, food deprivation experienced only years or months prior to death, which would presumably also increase an individual's risk of dying, may not be captured in bone collagen. In an analysis of individuals who experienced the Great Irish Famine (1845–1852), Beaumont et al. (2013a) expected higher $\delta^{15}N$ values for bone collagen samples but found no difference and attributed this to slow turnover rate in bone that averaged short-term changes in $\delta^{15}N$ values.

In addition to variation in diet, the difference in $\delta^{15}N$ values for bone collagen between burial types could also reflect the presence of migrants in the sample. During this period, rural-to-urban migration for labor opportunities (Dyer, 2002) and from harvest failure (Walter & Schofield, 1985) was common. Migrants to the city may exhibit slightly different isotope values compared to longer-term residents of London. However, though London had a $\delta^{15}N$-rich protein signature, it still plots with other contemporaneous English sites (Lakin 2008; Walter, DeWitte, Dupras, & Beaumont, 2019), suggesting migrants from areas within London's large catchment area likely did not have isotope values sufficiently different to substantially affect

our findings. Using only $\delta^{13}C$ and $\delta^{15}N$, it is not possible to determine whether migrants are more likely to be buried in attritional or famine-related interments (Montgomery, 2010; Montgomery, Evans, Chenery, Pashley, & Killgrove, 2010).

Sex-specific comparisons reveal no significant differences between burial types for either sex, suggesting that famine did not affect males and females differently. Females in attritional burials exhibit higher $\delta^{15}N$ values compared to females in famine burials; though the results are suggestive of an effect, they are not significant ($p=0.09$). Previous isotopic analysis of SRP98 shows that young females in Period 15 had higher $\delta^{13}C$ and $\delta^{15}N$ values compared to males, which was attributed to female-led migration (Lakin, 2010). During the Late Medieval Period, it was common for adolescents and young adults, particularly females (Goldberg, 2004), to travel to urban centers because of greater economic opportunities (Dyer, 2002; Hanawalt, 1995; Kowaleski, 2014; Lewis, 2016). However, as discussed above and contrary to Lakin's (2010) assessment, it is likely not possible to attribute this difference to migration using $\delta^{13}C$ and $\delta^{15}N$ isotope values alone.

4.2 Patterns in dentine collagen profiles

Incremental dentine analysis reveals that there is a higher proportion of individuals with fluctuating dentine profiles in famine burials compared to attritional burials, and that most of the fluctuations in attritional burials are gradual, occurring over several years, unlike the famine burials. Henderson, Lee-Thorp, and Loe (2014) used incremental dentine analysis to assess early dietary history of poor 18–19th century Londoners presumably not facing famine. A review of the dentine profiles from this study shows that, after weaning age (≈3 years), 9 of 42 individuals

exhibit an increase or decrease in $\delta^{15}N$ of at least 2‰ (noted in this study as a fluctuation). However, for all except one of these individuals, the changes are gradual, occurring over ≈4–5 years. The stable dentine profiles in the Henderson et al. (2014) study are similar to what was observed in the attritional burials in this study, suggesting that the more short-term fluctuating dentine profiles observed in famine burials may be unique to individuals facing famine.

Though it may not be possible to disentangle isotopic patterns resulting from nutritional stress (i.e., enriched nitrogen as a result of nutritional stress) or from dietary change (i.e., elevated nitrogen values due to more protein in the diet), some individuals exhibit $\delta^{13}C$ and $\delta^{15}N$ patterns that are consistent with an opposing covariance pattern observed in stable isotope studies of nutritional stress. This pattern is observed in more famine than attritional burials, and the presence of EHs in some individuals exhibiting this pattern further supports previous studies interpreting opposing covariance as being associated with nutritional stress. Similarly, in Sandberg, Sponheimer, Lee-Thorp, and Van Gerven's (2014) study of ancient Nubians, they find that more EHs formed during weaning rather than before or after, suggesting that systemic stress was experienced by these individuals during the weaning process. This supports our interpretation that the EHs formed during the opposing covariance pattern are associated with some kind of nutritional stress, as weaning can also be considered a type of nutritional stress.

The pattern, however, is also present in two attritional burials, though the pattern is less distinct, and is observed in individuals without evidence of EH formation, thus we cannot definitively associate opposing covariance of $\delta^{13}C$ and $\delta^{15}N$ with nutritional stress that is sufficient to cause EH. An analysis of EH and incremental dentine profiles of individuals who

experienced the Great Irish Famine (1845–1852) observed that the least amount of EHs formed during famine compared to before and after the event (Geber, 2014), indicating that nutritional stress may not necessarily result in EH.

5 Conclusions

Analyses of bone collagen comparing $\delta^{13}C$ and $\delta^{15}N$ values between attritional and famine burials indicate that individuals interred in attritional graves exhibit significantly higher $\delta^{15}N$ values compared to individuals in famine graves, with no significant difference in $\delta^{13}C$ values. Rather than directly reflecting catabolism of an individual's own tissue proteins during times of nutritional stress, these results may reflect differences in diet that occurred as a consequence of famine (e.g., different types or proportions of protein sources in the diet during famine because of limited access to food supplies). Sex-specific comparison of bone collagen reveals no significant differences between burial types for either sex, suggesting that famine did not affect males and females differently.

Analyses of incremental dentine collagen profiles reveal that individuals from famine burials exhibit more fluctuating $\delta^{13}C$ and $\delta^{15}N$ values during childhood compared to attritional burials, though no definitive pattern unique to famine burials could be identified. Some individuals in this sample, however, exhibit an opposing covariance pattern of $\delta^{13}C$ and $\delta^{15}N$ that has been identified in previous incremental analyses of nitrogen and carbon in the context of undernutrition, suggesting that these individuals may have experienced nutritional stress during childhood. Further, in some cases, the formation of EH is observed to have occurred in

conjunction with this patterning of $\delta^{13}C$ and $\delta^{15}N$, further supporting that concurrent covariance in $\delta^{13}C$ and $\delta^{15}N$ is reflective of undernutrition.

Additionally, isotopic values from bone collagen may not reflect nutritional stress experienced just prior to death because of slow tissue turnover rates. However, incremental dentine analysis may be useful for identifying dietary patterns or nutritional stress occurring during childhood that could have increased an individual's risk of death during famine, as indicated by the results of this study.

Finally, this study underlines the importance of incorporating multiple tissues and lines of evidence in stable isotope analyses to better understand the consequences of famine. Using different tissues can tell us about isotopic changes throughout the life course, rather than limiting analyses to broad averages prior to death. Furthermore, by including pathological information (e.g., EH) in conjunction with stable isotope analyses it may be possible to clarify patterns of fluctuating isotope values (e.g., fluctuations in isotope values as potential nutritional stress rather than dietary change). The integration of pathological data and isotope values could also be informative about the relationship between frailty and diet (i.e., if individuals who died from famine exhibit fluctuations in isotope patterns during childhood related to physiological stress), which could contribute to current research evaluating frailty and famine mortality.

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The views presented here are those of the authors and do not reflect the views of the Department of Defense and Defense POW/MIA Accounting Agency.

Data Sharing Statement

The data that support the findings are available as Supplemental Materials with this manuscript. Any additional data is available from the corresponding author upon reasonable request.

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Figure Legend

Figure 1: Plotted carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios for bulk bone collagen of rib samples for all individuals by burial type.

Figure 2: Boxplots of nitrogen ($\delta^{15}N$) isotope ratios for bulk bone collagen of rib samples for all individuals by burial type.

Figure 3: Plotted carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios for bulk bone collagen of rib samples for females and males by burial type.

Figure 4: Incremental dentine carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio profiles by estimated age of a first premolar from a young adult male (SRP98-30920, top) in a famine grave with the opposing covariance pattern at ≈3–7 years and a second premolar from an adult female (SRP98-10765, bottom) in an attritional grave with a stable pattern typical of dietary change. Bulk bone collagen values are independent of the x-axis (age).

Figure 5: Incremental dentine carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio profiles by estimated age of a first premolar from a young adult male (SRP98-30920) in a famine grave with an opposing covariance pattern at ≈3–7 years and black lines depicting enamel hypoplasia formation ages. Bulk bone collagen values are independent of the x-axis (age).

Figure 6: Incremental dentine carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio profiles by estimated age of a first premolar from an adult male (SRP98-20682) in a famine grave with an opposing covariance pattern at ≈4.5–8 years and black lines showing enamel hypoplasia formation ages. Bulk bone collagen values are independent of the x-axis (age).

Figure 7: Incremental dentine carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio profiles by estimated age of a first premolar from a young adult male (SRP98-9632, top) in a famine grave with an opposing covariance pattern at ≈6–8 years, and profiles of a first premolar from an adult male (SRP98-9789, bottom) in a famine grave with an opposing covariance pattern at ≈11 years until the tooth completes formation at 13.5 years. Bulk bone collagen values are independent of the x-axis (age).

Figure 8: Incremental dentine carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio profiles by estimated age of a second premolar from a young adult female (SRP98-32302) in a

famine grave with an opposing covariance pattern at ≈3.5–6 years. Bulk bone collagen values are independent of the x-axis (age).