Stress, sex, and plague: patterns of developmental stress and survival in pre- and post-Black Death London

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ABSTRACT:

OBJECTIVES: Previous research revealed declines in survivorship in London before the Black Death (*c.* 1346-1353), and improvements in survivorship following the epidemic. These trends indicate that there were declines in general levels of health before the Black Death and improvements thereof afterwards. This study expands on previous research by examining whether changes in survivorship were consistent between the sexes, and how patterns of developmental stress markers changed before and after the Black Death.

MATERIALS AND METHODS: This study uses samples from London cemeteries dated to one of three periods: Early Pre-Black Death (1000-1200 AD, n = 255), Late Pre-Black Death (1200-1250 AD, n = 247), or Post-Black Death (1350-1540 AD n = 329). Temporal trends in survivorship are assessed via Kaplan-Meier survival analysis, and trends in tibial length (as a proxy for stature) and linear enamel hypoplasia (LEH) are assessed using t-tests and Chi-square tests, respectively.

RESULTS: Survivorship for both sexes decreased before the Black Death and increased afterwards. For males, LEH frequencies increased and stature decreased before the epidemic, and LEH declined and stature increased after the Black Death. For females, the only significant change with respect to developmental stress markers was a decrease in stature after the Black Death.

CONCLUSIONS: These results might reflect variation between the sexes in sensitivity to stressors, the effects of nutrition on pubertal timing, disproportionate access to dietary resources for males in the aftermath of the Black Death, the disproportionate deaths of frail individuals during the epidemic, or some combination of these factors.

INTRODUCTION

Recent research has yielded important insights about the 14th-century Black Death, one of the most devastating epidemics in history and the first outbreak of what is often referred to as the Second Pandemic of Plague. Molecular evidence from 14th-century Black Death burials confirms the long-held (though previously strongly contested) assumption that the Black Death was caused by *Yersinia pestis*, the bacterium that causes bubonic plague in living populations (Bos et al., 2011; Haensch et al., 2010; Kacki et al., 2011; Raoult et al., 2000; Schuenemann et al., 2011). There is also molecular evidence that *Y. pestis* infected individuals in the Bronze age (Rasmussen et al., 2015), during the 6th-century AD Plague of Justinian (Harbeck et al., 2013; Wagner et al., 2014; Wiechmann and Grupe, 2005), and in outbreaks of plague subsequent to the Black Death in the medieval and early modern periods (Bos et al., 2016; Tran et al., 2011). Plague continues to kill people every year. During a recent outbreak in Madagascar, for example, there were nearly 500 reported cases and over 80 deaths (Bertherat, 2015). Plague has thus affected humans, at times severely, for over 5000 years.

Despite the interest that plague has generated among generations of scholars from a variety of disciplines, some of what is reported about the Black Death and other historic outbreaks of plague reflects the unexamined imposition of epidemiological and other patterns observed in modern outbreaks of plague onto the past. For example, it is often assumed that the Black Death was spread by rats and their fleas given that this was a common route of transmission in more recent outbreaks, but it is not yet clear how plague was transmitted in the medieval period (Ziegler, 2014). Assessing the true patterns of medieval plague epidemics and the context and consequences of past epidemics is hampered by the fact that most reconstructions have been based on data from historical documents, which are generally biased toward wealthy men. Recent bioarchaeological analyses, however, have clarified Black Death mortality patterns (at least in the context of medieval London) using skeletal samples that are more broadly representative of the once-living population than is true of historical documents (including, in particular, women, children, and the poor). This work has challenged assumptions that the Black Death killed indiscriminately (DeWitte and Hughes-Morey, 2012; DeWitte and Wood, 2008). Bioarchaeological studies are also clarifying the demographic and health context of the emergence of the Black Death and the effects that the epidemic had on the surviving population (DeWitte, 2014b; DeWitte, 2015).

This study expands upon previous bioarchaeological research that examined trends in demography prior to and following the Black Death. This research revealed declines in survivorship and increases in risks of mortality in London in the 13th century compared to the 11-12th centuries and thus, by inference, declines in general levels of health in the period leading up to the Black Death (DeWitte, 2015). This research also revealed improvements in survivorship and declines in risks of mortality, suggestive of improvements in health, in London following the Black Death, *c*. 1350-1540 (DeWitte, 2014b). Both studies of the demographic trends before and after the Black Death examined general population patterns using pooled-sex samples. However, there is reason to suspect that differences in survivorship trends in medieval London might have existed between males and females. Previous research suggests that females might have been less frail than males at the time of the Black Death (DeWitte, 2010), but that males faced lower risks of mortality just after the epidemic (Yaussy et al., 2016). This raises the question of whether observed population-level trends before and after the Black Death might mask underlying differences in patterns of health (or physiological stress) or demography between the sexes. Therefore, this study examines sex-based variation in temporal trends in survivorship to assess whether changes in demography (and thus health) before and after the epidemic were similar for males and females.

In addition to assessing demographic trends before and after the Black Death, research has also revealed temporal trends in periosteal new bone formation that are, perhaps paradoxically, consistent with improvements in health following the Black Death (DeWitte, 2014a). Specifically, there were increased proportions of people who were both older (above 45 years of age) and had periosteal new bone formation after the Black Death than was true before the epidemic. That is, people were apparently living longer following the epidemic but consequently exhibiting relatively poor skeletal condition at late adult ages, perhaps because they spent more years accumulating the effects of non-fatal physiological stressors that lead to periosteal lesions. These results suggest that tradeoffs "of mortality for morbidity" that have been observed in some living populations (see also: Bonneux et al., 1994: p. 20; see also Crimmins, 2004; Crimmins et al., 1994; Molla et al., 2003) might also have existed in the past. However, given that periosteal lesions can occur in response to a wide variety of factors (e.g. trauma, nutritional deficiencies, local or systemic infection) at any age, the previous study did not address how the Black Death specifically affected patterns of physiological stress among subadults, arguably one of the most vulnerable segments of a population. To further our understanding of changes in physiological stress before and after the Black Death, this study examines temporal trends (early pre-Black Death vs. late pre-Black Death trends, and pre- vs. post-Black Death trends) in developmental stress markers (linear enamel hypoplasia and tibial length as a proxy for adult stature). Further, as with the analysis of survivorship, this study also examines sex-based variation in temporal trends in these stress markers for the reasons outlined above.

MATERIALS AND METHODS

Skeletal samples

All skeletal samples (n = 831) for this study come from medieval London cemeteries and are curated at the Museum of London Centre for Human Bioarchaeology. To examine trends in developmental stress and survival before the Black Death, I compared samples of individuals who are clearly dated to one of two non-overlapping Pre-Black Death periods: an Early Pre-Black Death period that dates from the 11^{th} through the 12^{th} centuries AD, and a Late Pre-Black Death period that dates to the first half of the 13^{th} century. To assess changes in patterns of stress and survivorship in the aftermath of the Black Death, I compared individuals in burials dated exclusively to the Late Pre-Black Death period to those buried in the period immediately following the epidemic (Post-Black Death, *c.* 1350-1540). The sample sizes used from each cemetery and their corresponding time periods are shown in Table 1.

[Insert Table 1 here]

Pre-Black Death sample: St. Mary Spital, Guildhall Yard, and St. Nicholas Shambles The pre-Black Death sample was drawn from three medieval London cemeteries, St. Mary Spital (SRP98), Guildhall Yard, and St. Nicholas Shambles. The pre-Black Death sample includes only individuals who are dated to one of two distinct pre-Black Death periods: Early Pre-Black Death (*c.* 1000-1200; n = 255 and Late Pre-Black Death (*c.* 1200-1250, n = 247). Based on stratigraphic, documentary, and artifact evidence, St. Nicholas Shambles dates to the 11-12th centuries, and Guildhall Yard dates to the 11th – early 13th centuries (Bowsher et al., 2007; Schofield, 1997; White, 1988). Burials in Guildhall Yard date to two periods, 1050-1150 and 1140-1230. More precise dates within each of those two periods are not available, thus it is not possible to identify individuals from the latter period (1140-1230) who were buried in the 12th *versus* the 13th century. Therefore, individuals from the 1140-1230 period were excluded in order to prevent temporal overlap between the Early and Late Pre-Black Death samples. This study includes 133 individuals from St. Nicholas Shambles and 13 from Guildhall Yard; this sample represents all of the individuals in these two cemeteries dated to the Early Pre-Black Death period who were preserved well enough to provide data on age or stress markers using the methods described below. The main cemetery (SRP98) associated with the hospital and priory of St. Mary Spital has been divided into four periods based on stratigraphic evidence and Bayesian radiocarbon dating: Period 14 (c. 1120-1200), Period 15 (c. 1200-1250), Period 16 (c. 1250-1400) and Period 17 (c. 1400-1539). Within each period, there are both single and multiple burials (Connell et al., 2012; Sidell et al., 2007). About half of the burials in SRP are single interments (Type A burials). Types B and C burials consist of single horizontal layers of 2-7 bodies or stacks of 2-11 bodies, respectively. Type D consists of multi-layered burials in which 8-45 bodies are buried in horizontal rows stacked on top of each other. Type D burials are associated with famine-related catastrophic mortality, and types A, B, and C are viewed as representing normal ("attritional") mortality (Connell et al., 2012). However, this study takes a conservative approach by restricting analyses to the Type A burials. For this study, I selected a stratified random sample of 356 individuals from the Type A burials: 109 from Period 14 for the Early Pre-Black Death sample and 247 from Period 15 for the Late Pre-Black Death sample.

These individuals were preserved well enough to provide data on age or stress markers. Though St. Mary Spital was established for the purpose of treating the poor, migrants, and for providing a safe place for childbirth, the associated cemetery served for burials for members of the religious community (i.e., monks and lay sisters) and wealthy benefactors, and is considered to primarily be a secular cemetery (Connell et al., 2012). The first hospital at the site had an associated cemetery (Spital Square) that was exclusively used by the infirmary from 1197 to 1280 (Thomas et al., 1997). However, Spital Square cemetery is not included in this study (Spital Square and St. Mary Spital cemeteries are distinct assemblages). The hospital was re-founded in 1235 on a plot of land that included the Spital Square cemetery that was already in use. It is suggested that St. Mary Spital cemetery was not used to bury those who died in the infirmary until after 1280 (given that the infirmary used the Spital Square cemetery described above until that time) (Connell et al., 2012: p. 4-5). Thus St. Mary Spital burials that pre-date 1280 (i.e. burials from Periods 14 and 15) are not likely biased toward infirmary patients. The combined Pre-Black Death sample of 502 individuals from St. Mary Spital, Guildhall Yard, and St. Nicholas Shambles contains both sexes, and a combination of low- and high-status lay individuals and members of religious communities.

Post-Black Death sample: St. Mary Graces and St. Mary Spital The Post-Black Death sample (n = 329) comes from St. Mary Spital Period 17 (c. 1400-1540) burials and the cemetery associated with the Cistercian Abbey of St. Mary Grace. For the Post-Black Death sample, I selected a random sample of 212 individuals from among the Type A attritional burials from Period 17 who were preserved well enough to provide data on age or stress markers. St. Mary Graces was established in London in 1350, soon after the Black Death ended, and it was in use until the Reformation in 1538 (Grainger and Hawkins, 1988; Grainger et al., 2008). Burials in St. Mary Graces include both high and low status individuals and monks (Grainger and Phillpotts, 2011). There are also victims of 14th-century plague (the plague of 1361 or a subsequent outbreak) in an area spatially distinct from the rest of the St. Mary Graces burials. These putative plague burials are close to the Black Death burials in the underlying East Smithfield cemetery (*c.* 1349-1350) and far from the Abbey, whereas the non-plague burials are clustered close to or are within the Abbey (Bos et al., 2016; Gilchrist and Sloane, 2005; Grainger and Phillpotts, 2011; Sloane, 2011). An unusually high proportion of people (49%) in the St. Mary Graces plague burials were buried in coffins; this high proportion is similar to that observed in East Smithfield, but more than twice that observed in the non-plague burials in St. Mary Graces and in other normal medieval samples. During medieval plague epidemics, many cities ordered the use of coffins to prevent corruption from rotting plague victims (Creighton, 1891), and the high use of coffins in East Smithfield and the St. Mary Graces plague burials is consistent with these ancient public health measures. Recent ancient DNA evidence has confirmed the presence of *Y. pestis* in an individual buried in the plague area of St. Mary Graces (Bos et al., 2016). To avoid the potential for plague mortality patterns to obscure non-epidemic patterns, this study uses a sample of 117 individuals from among the non-plague St. Mary Graces burials that were preserved well enough to provide data on age or stress markers using the methods described below. As is true of the Pre-Black Death sample, the combined post-Black Death sample from St. Mary Spital and St. Mary Graces contains both sexes, and a combination of low and high status lay individuals and members of religious communities. Period 17 burials from St. Mary Spital may include more infirmary patients than those from Periods 14 and 15; the potential effects of this on the results of this study are discussed below.

It should be noted that the samples used in this study are subsamples of the total number of individuals originally buried in the cemeteries. Excavation of St. Mary Spital yielded 10,516 individuals, over half of the estimated 18,000 or so individuals originally buried in the cemetery (Connell et al., 2012). Of the individuals excavated, the Museum of London recorded 5387 and made them available to researchers. The Period 16 burials and the type B, C, and D burials from all Periods were excluded from this study to allow for a conservative analysis of non-catastrophic mortality patterns. Of the available attritional (Type A) burials from Periods 14, 15, and 17 (n = 250, 291, and 432, respectively), I selected samples of 109, 247, and 212 individuals, respectively, who provided data on age or stress markers. Including all available individuals was not feasible, particularly in light of the temporary closure of the Museum of London Centre for Human Bioarchaeology (at the time of writing, the Centre is projected to be closed to researchers until 2021, Jelena Bekvalac, pers. comm.). Nearly all of the St. Nicholas Shambles cemetery area was excavated and was available for analysis (White, 1988), and archaeologists conducted a full excavation of the Guildhall site (Bowsher et al., 2007). However, this study includes only those individuals from both cemeteries dated to 1000-1200 for whom it was possible to estimate age or score stress markers. According to Grainger and Phillpotts (2011), excavation of the external St. Mary Grace's cemetery (i.e. the burials outside the Abbey buildings) yielded a "substantial portion" (p. 98) of the total number buried there, and of those originally buried within the church, 50-80% were excavated (p. 100). This study includes all excavated individuals from St. Mary Graces, exclusive of the plague burials, for whom age or lesions could be scored. Readers should note that the samples might be biased to an unknown degree and thus the results presented here should be viewed with the typical caution reserved for bioarchaeological analyses.

Age Estimation

Adult ages were estimated using transition analysis (Boldsen et al., 2002), which minimizes the age-mimicry associated with conventional methods of age estimation and provides point estimates of age, even for older adults (i.e. rather than a broad terminal adult age category). In transition analysis, data from a known-age reference collection are used to obtain the conditional probability, $Pr(c_j|a)$, that a skeleton will exhibit a particular age indicator stage or suite of age indicator stages given the individual's known age. This conditional probability is combined, using Bayes' theorem, with a prior distribution of ages at death to determine the posterior probability that a skeleton in the cemetery sample died at a certain age given that it displays particular age indicator stages. By combining the conditional probability, $Pr(c_j|a)$, from a known-age reference sample, with a prior distribution of ages at death, transition analysis avoids imposing the age distribution of the reference sample on the target sample (Boldsen et al., 2002). For this study, transition analysis was applied to skeletal age indicators on the pubic symphysis and the iliac auricular surface and to cranial suture closure as described by Boldsen et al. (2002). The Anthropological Database, Odense University (ADBOU) Age Estimation software was used to determine individual ages-at-death. The ADBOU program uses a conditional probability estimated from the Smithsonian Institution's Terry Collection, and I selected an informative prior distribution of ages at death based on data from 17th-century Danish rural parish records (the Gompertz-Makeham parameter estimates for this "archaeological" prior are: $\alpha_1 = 0.01273$, $\alpha_2 = 0.00002478$, and $\beta = 0.1060$; Jesper Boldsen, pers. comm. 9/3/08). For the survival analyses described below, point estimates of adult age were used without their associated errors to estimate differences in survivorship. Further, though the archaeological prior represents a generalized preindustrial mortality curve and is thus appropriate for medieval London (Bullock et al., 2013), use of this prior in the ADBOU software runs the risk of underestimating the ages of people 70 years of age and older (the uniform prior tends to lead to overrepresentation of the oldest ages and the forensic prior is not appropriate for use for ancient populations) (Milner and Boldsen, 2012). Underestimation of the oldest ages is not a concern for this study as the method was used consistently across all samples, and the focus of this study is population-wide patterns (i.e. rather than on the numerical values of individual age estimates themselves). Readers should view the estimated values as indicative of general trends rather than attending to the specific numerical values.

For all analyses in this study, the minimum age for inclusion in the adult sample is 15 years. Subadults were included in the analyses of temporal trends in enamel hypoplasia (for the pooled-sex sample) but not in analyses of adult stature or survivorship. Ages for subadult individuals (i.e. those individuals for whom all epiphyses had not yet fused) were estimated based on epiphyseal fusion, and dental development and eruption (Buikstra and Ubelaker, 1994; Gustafson and Koch, 1974; Moorrees et al., 1969; Scheuer et al., 1980; Scheuer and Black, 2000; Smith, 1991). The adult age-at-death distributions from each period are shown in Table 2.

[Insert Table 2 here]

Sex determination

Sex was determined for adults based on sexually dimorphic features of the skull and pelvis using the standards described in Buikstra and Ubelaker (1994). The following dimorphic features of the skull and pelvis were scored: glabella/supraorbital ridge, supraorbital margin, mastoid process, external occipital protruberance/nuchal crest, mental eminence, ventral arc of the pubis, subpubic concavity, ischiopubic ramus ridge, and the greater sciatic notch. The accuracy of these individual skeletal features, or various combinations thereof, for the purposes of sex determination has been shown to range from 68 to over 96 percent (Graw et al., 1999; Phenice, 1969; Rogers, 2005; Sutherland and Suchey, 1991; Ubelaker and Volk, 2002; Walker, 2005; Williams and Rogers, 2006). Multiple skeletal indicators of sex were used for this study given that including more than one indicator improves the accuracy of sex determination (Meindl et al., 1985; Rogers, 2005; Walker, 2008; Williams and Rogers, 2006). Because sex determinations based on features of the pelvis alone have been shown to be more accurate than those based on features of the skull alone (Meindl et al., 1985; Walrath et al., 2004), for individuals in this study for which the skull and pelvis indicated different sexes, the pelvic scores were subjectively weighted more heavily than features of the skull. This weighting occurred in cases in which the skull of an individual was ambiguous with respect to sex, but the pelvis was strongly one sex or the other; in these cases, the individual was assigned the sex indicated by the pelvis. The possible presence of misclassified individuals within the samples used for this study would tend to underestimate differences between the sexes in temporal patterns of survivorship and stress markers.

Developmental Stress markers

Linear enamel hypoplasia Linear enamel hypoplasia is a tooth enamel defect caused by the disruption of enamel formation during childhood as a result of various stressors such as infection or malnutrition (Dahlberg, 1991; Huss-Ashmore et al., 1982; Roberts and Manchester, 2005). Previous research has suggested that enamel hypoplasias were associated with elevated risks of mortality during the Black Death in London and under non-epidemic, normal medieval mortality conditions (DeWitte and Wood, 2008). Linear enamel hypoplasias appear as horizontal shallow grooves of varying width on the surface of the tooth. For this study, linear enamel hypoplasias were identified macroscopically, under good lighting conditions, on the buccal surface of the permanent mandibular canines, which have relatively long developmental time-spans and are highly sensitive to physiological stress (Goodman et al., 1980; Huss-Ashmore et al., 1982; Santos and Coimbra, 1999). Left permanent mandibular canines were assessed when present, but data from right canines were included in cases where left canines were missing or damaged. LEH were assessed only on fully mineralized crowns of permanent mandibular canines, and only canines with little or no wear were included in the analyses. Including some individuals in the sample who have minimal wear runs the risk of underestimating the prevalence of LEH, but does allow for assessing trends across a wider range of ages (i.e. this analysis is not limited to children and young adults). The possible effect of age (and thus wear) on observed LEH frequency is accounted for using binary logistic regression, as detailed below. Linear enamel hypoplasia were scored as “present” if one or more lesions on the surface of the tooth were palpable and visible to the naked eye. By using this approach, it is likely that enamel defects are underestimated in this study, as Hassett (2014) has found that "naked-eye" methods of assessing LEH identify fewer defects compared to microscopic approaches. However, given that the naked-eye approach was used consistently for all individuals in the samples for this study, and that this study is concerned with presence/absence rather than number of LEH, this should not severely affect the inferences made about temporal patterns of or sex differences in LEH.

Adult stature Adult stature reflects, among other things, exposure to chronic stress during development (Haviland, 1967; Powell, 1988; Roberts and Manchester, 2005; Steckel, 1995). Children who are exposed to physiological stress, such as malnutrition or infection, during development must at least temporarily expend energy resources primarily on basic tissue maintenance or the immune response rather than growth and development. Therefore, short adult stature, relative to other individuals within the population, can indicate poor health or poor nutrition during developmental. Bioarchaeological studies of stature often involve the estimation of stature from bone measurements using regression functions derived from known-stature reference samples. However, this approach is complicated by between-population differences in body proportion and stature. Because I am not interested in adult stature *per se*, but am using it as an indicator of exposure to physiological stress during the developmental period, I avoid the potential problems associated with estimating stature by directly comparing long bone lengths across time periods. For this study, I used adult tibia length as a proxy for stature. Larger sample sizes of tibiae were available for analyses; further, there is evidence that the tibia is more sensitive than other long bones to environmental stress during growth and development (Jantz and Jantz, 1999). The maximum length of the tibia was measured in centimeters using an osteometric board (Buikstra and Ubelaker, 1994). Previous research has shown elevated risks of mortality for short individuals, using long-bone lengths as a proxy for stature, during the Black Death in London (but not under conditions of normal medieval mortality, at least before the Black Death) (DeWitte and Hughes-Morey, 2012).

Analyses of trends in LEH and stature were previously done using just the St. Mary Graces cemetery (including the burial types B and C described above) (Connell et al., 2012). Though there was some variation across periods in estimated stature (Redfern, 2012), Gray Jones

(2012: p. 226) concluded that there was "little difference in attained height" between the four periods of use in St. Mary Spital. Similarly, minimal changes in LEH frequencies were observed across the Early Pre-Black Death, Late Pre-Black Death, and Post-Black Death time periods in St. Mary Spital (Connell, 2012).

Statistical Analyses

Trends in Stress Markers Chi-square tests were performed to assess whether LEH frequencies changed over time for pooled-sex samples (these include subadults) and for adult males and female separately. Given the possibility that age-related dental wear can affect observed frequencies of LEH, the association between age and LEH was assessed with binary logistic regression and using a pooled sample of all individuals across all time periods with mandibular canines that could be scored for LEH. Temporal trends in adult tibia length were assessed for adult males and females separately using t-tests. Chi-square and t-tests were performed in SPSS version 24.

Kaplan-Meier Survival Analysis

Pre-Black Death trends in survival: As in previous work on trends in survival before the Black Death (DeWitte, 2015), the effect of time period on survival (Early Pre-Black Death *c.* 11-12th century = 0; Late Pre-Black Death *c.* 13th century = 1) was assessed using Kaplan-Meier survival analysis with a log rank test and using pooled data on age from both Pre-Black Death time periods. Analysis was performed using SPSS version 24. In order to compare the results of this study with those obtained with previous analyses, Kaplan-Meier survival analysis was performed only on adults 15 years of age and above. To confirm that previously observed patterns of pre-

Black Death survivorship were obtained using a sample size larger than that available for the earlier study (DeWitte, 2015), analyses were initially conducted with pooled data from both sexes. Analyses were then done separately for adult males and females to determine whether any estimated changes in survivorship were consistent between the sexes.

Late Pre- vs. post-Black Death survival: To assess differences in survivorship between the Late Pre-Black Death and Post-Black Death periods, the effect of time period on survival (Late Pre-Black Death = 0, Post-Black Death = 1) was assessed using Kaplan-Meier survival analysis with a log rank test and using pooled data on age from both time periods. As with the analysis of Pre-Black Death trends in survivorship, to confirm that previously observed patterns of post-Black Death survivorship (DeWitte, 2014b) are obtained using a post-Black Death sample size larger than that available for the earlier study and a pre-Black Death sample that excludes Early Pre-Black Death burials, analyses of Late Pre- vs. Post-Black Death survivorship were initially conducted with pooled data from both sexes. To assess whether the increase in adult survivorship following the Black Death found in the previous study (DeWitte, 2014b) was consistent between the sexes, Kaplan-Meier analysis was then applied separately to males and females from all cemeteries.

For all analyses, p-values less than 0.1 are considered suggestive of a trend.

RESULTS

Linear enamel hypoplasia The temporal trends in frequencies of LEH and the results of corresponding Chi-square tests are shown in Table 3; the pooled samples include data from subadults, whereas those for males and females include only adults. In the pre-Black Death period, when all ages and both sexes are considered together, there is a significantly higher frequency of LEH in the 13th century compared to the 11-12th centuries. During this period, an increase in LEH frequency of a similar magnitude is also observed among adult males, but not in females. LEH frequencies remain fairly constant for female across the two pre-Black Death periods. Comparison of LEH frequencies between the Late Pre-Black Death *vs.* Post-Black Death periods using all ages and sexes combined reveals a significant decrease in the frequency of LEH after the Black Death. A similar significant drop in LEH following the Black Death is also observed among the males. Frequencies of LEH decline after the epidemic for females as well, but this decline is not significant and is less dramatic than that observed in males. The results of binary logistic regression of the association between age and LEH reveal that there is no significant association between the two variables (odds ratio = 0.998, 95% confidence interval = 0.986 – 1.011, $p = 0.77$). This suggests that the observed trends in LEH frequencies are not artifacts of differences in age-at-death distributions across the subsamples used in this study.

[Insert Table 3 here]

Stature The temporal trends in male and female tibia length, as a proxy for stature, are shown in Table 4; these analyses only include adults. In the Pre-Black Death period, male stature decreases significantly in the Late Pre-Black Death period compared to the Early Pre-Black Death period. Female stature, however, increases from the Early to Late Pre-Black Death periods, but not significantly so. With respect to Late Pre-Black Death vs. Post-Black Death trends, male stature increases significantly following the epidemic, whereas female stature *decreases* significantly across the two time periods.

[Insert Table 4 here]

Survivorship The results of Kaplan-Meier survival analyses (mean survival times and their corresponding 95% confidence intervals) are shown in Table 5; these analyses include only individuals 15 years of age or older. The pooled-sex results (which include individuals of indeterminate sex) are consistent with findings from previous studies of declines in survivorship in the 13th century compared to the 11-12th centuries (DeWitte, 2015) and of improvements in survivorship following the Black Death compared to pre-Black Death conditions (DeWitte, 2014b). The results for both sexes individually mirror those for the sexes combined, with a decline in survivorship before the Black Death and an increase in survivorship after the epidemic.

[Insert Table 5 here]

DISCUSSION

These results suggest similar temporal trends in survivorship for both sexes but distinct male *vs.* female patterns of physiological stress before and after the Black Death.

Trends in Survivorship The survivorship results reveal reductions in survivorship (and, by inference, health) for both females and males in the Late Pre-Black Death period compared to the Early Pre-Black Death period in London. These results are consistent with previous findings that were based on a pooled-sex sample and that were not apparently an artifact of changes in birth rates (DeWitte, 2015). As noted in that previous study, there is a lag of several decades between the latest date of the Late Pre-Black Death sample and the emergence of the Black Death. However, there is historical evidence for the interim (beginning in 1270), and though generally limited to males, it reveals a substantial demographic decline that began approximately two generations before the Black Death (Smith, 2012:49). This suggests that any deterioration in demography and health that occurred in the beginning of the 13^{th} century did not reverse before the Black Death. Together, the bioarchaeological and historical data suggest a population in relatively poor general health and thus vulnerable to the effects of the Black Death.

These demographic trends coincide with a variety of factors that might have increased frailty in the pre-Black Death population. The Pre-Black Death skeletal samples for this study date to a period that falls within and at the end of the Medieval Warm Epoch. The period from 1000-1200 AD was relatively warm and associated with economic and demographic growth in England, but cooling temperatures in the 13^{th} and 14^{th} centuries resulted in widespread famines (Brooke, 2014; Büntgen et al., 2011; Campbell, 2016; Galloway, 1986). Among these disasters was the Great Famine of 1315-1317, which killed an estimated 10-15% of the population of England (DeWitte and Slavin, 2013). This was followed by the Great Bovine Pestilence, which killed 62 percent of bovines in England and Wales between 1319-1320 and led to long term dairy depravations (DeWitte and Slavin, 2013; Jordan, 1996; Slavin, 2012). Population growth in the 13^{th} century continued as the limits of arable land were reached, and as a result grain prices and rents increased, and real wages fell (Rigby, 2006). These conditions produced increasing social inequity and deteriorating standards of living for a large proportion of the English population (Campbell, 2016; Rigby, 2006). In addition to its potential direct effects on health, famine also drove migration into London (Farr, 1846; Stothers, 2000), and some immigrants might have already been in poor health or were vulnerable to endemic disease in London upon their arrival. Declines in health before the Black Death might have resulted directly from famine, attendant increased risk of disease, increased migration of vulnerable people, or the interaction of these factors.

The results of this study also reveal increased survivorship (and, again, by inference, increases in general health) for both females and males after the epidemic. This is also consistent with previous findings using pooled-sex samples (DeWitte, 2014b). As noted above, St. Mary Spital Period 17 may include more infirmary patients than those from the pre-Black Death period, and thus this study may underestimate improvements in survivorship. Given that people of all ages, including reproductive-aged individuals, with relatively high frailty were apparently at elevated risks of mortality during the Black Death (DeWitte and Wood, 2008), the epidemic might have affected genetic variation with respect to disease susceptibility or immune competence and thus acted to reduce average levels of frailty in the surviving population. Post-Black Death demographic changes might represent a "harvesting" effect of the epidemic (i.e. an increase in mortality among people with compromised health (Sawchuk, 2010)). Alternatively, the Black Death might have shaped population patterns by altering exogenous factors that affected health and demography. There is evidence from historical documents that standards of living in England improved after the epidemic. The severe shortage of laborers produced by the Black Death drove increases in wages and declines in prices for food, goods, and housing

(Bailey, 1996). By the late 15th century, for example, real wages were at least three times higher than they had been at the beginning of the 14th century (Dyer, 2005). To counter the post-epidemic mobility of workers, employers also increased payments in kind, including extra food, to attract and retain workers (Bailey, 1996). These changes following the Black Death resulted in improvements in housing and diet for people of all social status levels, but perhaps most important were the decreases in social inequities in access to food that presumably substantially benefitted the lower status people who made up the bulk of the English populace (Dyer, 2002; Hatcher, 1977; Poos, 1991; Postan, 1950; Rappaport, 1989; Stone, 2006). After the epidemic, people spent more money on food and ate higher quantities of relatively high quality wheat bread and fresh meat and fish, and these changes might have improved the nutritional quality of the English diet in general (Dyer, 2005). Given how strongly nutritional status affects immune competence (Scrimshaw, 2003), dietary improvements in particular might have acted to improve health following the Black Death.

Patterns of Physiological Stress The analyses of LEH and stature suggest that there was an increase in the exposure of males to childhood physiological stress in the Late Pre-Black Death period and a decline thereof following the Black Death (as noted above, the possible inclusion of more infirmary burials in St. Mary Spital Period 17 compared to Periods 14 and 15, might mean this study underestimates improvements in LEH and stature after the epidemic). These trends are consistent with the survivorship results from this and previous studies. The congruence of these results might reflect a relatively straightforward association between developmental stress early in life and adult survivorship for males during the medieval period. Repeated famines (Farr, 1846), disease, or other deleterious factors in the Late Pre-Black Death period may have negatively affected growth and development in males, which in turn adversely affected adult survivorship. For example, malnutrition *in utero* and during early childhood can stunt growth and have long-term or permanent negative effects on immune function and thus increase risks of mortality from infectious disease in adulthood (Moore, 2016; Moore et al., 1999; Palmer, 2011; Spencer, 2013; Sullivan et al., 1993). Alternatively, stress markers frequencies and survivorship in this period might reflect the same underlying factor without the two necessarily being directly causally linked (e.g., experiencing famine during both childhood and adulthood).

In the Post-Black Death population, improvements in standards of living, including diet (Bailey, 1996; Dyer, 2005) might have reduced the exposure of male children to physiological stress, which in turn allowed for enhanced adult male survivorship. Or, such improvements might have reduced exposure to developmental stress and enhanced adult survivorship for males without the two necessarily being causally linked. Alternatively, the disproportionate deaths of frail individuals during the Black Death might have increased the proportion of males who were intrinsically robust and thus able to both resist physiological stressors in childhood (and thus not form LEH or experience growth disruption) and survive longer as adults. Given that most of the individuals in the Post-Black Death sample are not survivors of the epidemic but are descended from survivors, this explanation of observed long-term trends in stress markers presumes a genetic component to frailty. If this were the case, it is not clear why the same effect was not observed among the females in this study. These results might also reflect migration into London after the epidemic. According to Dyer (2005) migration likely increased after Black Death as an expression of resistance against restrictions enacted under labor laws in England, such as attempts to prevent increases in wages after 1349. Numerous studies in a variety of different modern contexts have found evidence that international and within-country migrants are in better health and face reduced risks of mortality compared to locals (Anson, 2004; Tong and Piotrowski, 2012; Wallace and Kulu, 2014). This "healthy migrant effect" might occur because those who successfully migrate are a select sample of healthy individuals. It is possible that increases in migration following the Black Death introduced large numbers of healthy individuals, thus leading to improvements in health and mortality in the City in general. With respect to the observed increases in male stature, there is evidence from more recent contexts that migrants to urban areas are taller than urban and rural non-migrants (e.g. in mid-20th century Aberdeen, Scotland; Illsley et al., 1963). However, socioeconomic status might be a confounder in such analyses (Bogin, 1988). Further, this possibility does not explain the observed trends in stature for females. There is evidence that rural-urban migration in medieval England was disproportionately female (Goldberg, 1986; Kowaleski, 2013). Perhaps there was also variation in the composition of male *vs.* female cohorts of migrants to London that shaped the patterns observed in this study. Possible differences between male vs. female migrants might be addressed by future work incorporating isotopic signatures of migration.

The picture that emerges from this study for females is not as seemingly straightforward as that for males. As detailed above, the survivorship trends for females before and after the Black Death are similar to those for males, and consistent with previous findings (DeWitte, 2014b; DeWitte, 2015). If we take estimated mean survival times at face value, female survivorship does not appear to have increased to the same extent as did that of males following the Black Death. This might reflect lower risks of adult mortality for males compared to females following the epidemic, as was previously estimated for a subset of the sample used in this study (Yaussy et al., 2016). However, given the extent of overlap between the 95% confidence intervals for male and female mean survival time in the Post-Black Death period, and the errors associated with age-estimation, the difference in mean survival time might not accurately reflect the magnitude of the sex difference in survivorship. Perhaps more importantly, female stature remains unchanged across the two Pre-Black Death periods, but in dramatic contrast with observed trends in males, female stature *decreases* following the Black Death. Further, in contrast with the pattern revealed for males, LEH frequencies for females change minimally before the Black Death, and though they drop following the Black Death, they do not change significantly or to the same extent seen in males across these time periods.

In the Pre-Black Death period, female survivorship declines even though frequencies of LEH and stature do not change substantially. This suggests that females, like males, experienced elevated risks of mortality in adulthood in the first half of the 13th century, but that perhaps adult risks for females were not associated with stress experienced during childhood as might have been the case for males. It is possible that in the pre-Black Death population, females were better buffered against physiological stress (i.e. they were less sensitive to environmental conditions) during childhood compared to males, but perhaps that buffering was not sufficient in adulthood in the face of repeated famines and other factors that negatively affected adult health. Greater buffering of females has been suggested previously to explain sex differences observed among living individuals and in skeletal samples (e.g., King et al., 2005; Relethford and Lees, 1981; Vercellotti et al., 2011; Zakrzewski, 2003; also see reviews by Guatelli-Steinberg and Lukacs, 1999; Stinson, 1985). Alternatively, it is possible that the lack of significant changes in stress markers among females before the epidemic reflects *greater* vulnerability of female children – i.e. rates of LEH and stature remain unchanged among the adult female sample because the frailest females died in childhood upon exposure to stressors that cause growth disruption and thus did not enter the skeletal sample as adults with the associated stress markers. These varying possibilities highlight the complexities of interpreting skeletal lesions in samples of the dead (DeWitte and Stojanowski, 2015; Wood et al., 1992).

In the Post-Black Death period, the apparent decrease in female stature following the epidemic might indicate increased exposure to developmental stress for females in the aftermath of the epidemic, and perhaps, by inference, declines in health. There is evidence that female children and adolescents in urban in medieval England were more vulnerable to infection and respiratory disease than their male peers (Lewis, 2016). It is possible that the decrease in female tibial length in the post-Black Death sample reflects a greater proportion of infirmary patient burials in St. Mary Spital Period 17 burials. However, this possibility does not resolve the apparent contradiction in the trends in female survivorship *vs*. tibial length. That is, given that survivorship is reflective of underlying health, if observed mean tibial length decreased among females in the post-Black Death sample because of the inclusion of infirmary patients (i.e. a greater proportion of "unhealthy" individuals), presumably estimated female survivorship would also have declined, not increased as observed in this study. Viewing the estimated changes in stature in light of the estimated improvements in survivorship for females after the Black Death might indicate that females were relatively well buffered in the post-epidemic population. Perhaps they were not buffered against experiencing physiological stress sufficient to cause growth interruption in childhood, but rather were buffered against dying from the associated causes or from suffering long-term detrimental effects (e.g., reduced immune competence). The apparent lack of detrimental effect of this decrease in stature on adult female survivorship in the post-Black Death population is consistent with previous findings that short stature was not associated with elevated risk of mortality under normal medieval mortality conditions (though it was found to be associated with elevated risks of mortality during the Black Death) (DeWitte and Hughes-Morey, 2012).

Alternatively, the reductions in female stature following the Black Death might actually reflect improvements in diet or health following the epidemic. In contemporary populations, improvements in nutrition and reduced disease burden have been associated with earlier menarche (Karapanou and Papadimitriou, 2010; Sohn, 2016). Further, in some contemporary populations, positive associations have been found between age at menarche and height (though it should be noted this positive relationship appears to be true for industrialized countries but not for small-scale and agrarian populations in which it has been assessed) (McIntyre, 2011; McIntyre and Kacerosky, 2011). If nutritional status or disease burden improved substantially following the Black Death in London, this might have resulted in earlier average age at menarche in the post-epidemic population and thus earlier cessation of growth in females. A recent analysis of pubertal timing in medieval England revealed later average age at menarche in London compared to other sites included in the study, and this might reflect the effects of factors such as poor diet and exposure to disease in the city (Lewis, 2016); however, temporal trends (or a lack thereof) were not reported. Future work assessing average age at menarche before and after the Black Death might help to clarify the trends in stature observed in this study.

The post-Black Death patterns might alternatively suggest that males benefitted disproportionately from improvements in standards of living, including better diets, following the epidemic. This mechanism was suggested (though in the opposite direction, i.e. favoring women) by Arcini (2016) to explain significant increases in estimated mean stature for females following the Black Death in Sweden (from 160.2 to 162.7 cm), but smaller and non-significant changes in male stature (from 171.5 to 172.5 cm). If a sex difference in access to resources in favor of males occurred in London following the Black Death, the results of this study suggest that it produced positive outcomes for males with respect to growth faltering in childhood compared to females. Alternatively, if males were less well-buffered than females, perhaps they more responsive than females to improvements in diet after Black Death even if males did not have disproportionate access to dietary resources. This would not explain, however, why female stature declined after the Black Death. Future work incorporating stable isotope analyses of diet may allow for an evaluation of sex differences (or a lack thereof) in diet in the aftermath of the Black Death in London.

Given evidence that short stature and LEH were associated with elevated risks of mortality during the Black Death (DeWitte and Hughes-Morey, 2012; DeWitte and Wood, 2008), the difference in trends in these stress markers, particularly stature, between the sexes following the Black Death might reflect the effect of a greater proportion of frail males having died during the Black Death than was true of females (DeWitte, 2010). This might have resulted in a lower proportion of short males who survived the Black Death compared to females and thus an increase in male stature without similar increases for females in the aftermath of the epidemic.

CONCLUSION

The results of this study indicate that previously estimated population-wide declines in adult survivorship before the 14^{th}-century Black Death and improvements thereof following the epidemic occurred among both males and females in medieval London. Pre- and Post-Black Death trends in developmental stress markers (LEH and stature) among males are consistent with these demographic trends, and indicate that males experienced increases in developmental stress before the Black Death but decreases afterwards. The trends in stress markers for females, however, diverge from those of males. For females, there were no apparent significant changes in developmental stress prior to the Black Death, even though adult female survivorship declined. However, developmental stress as indicated by stature appears to have increased after the epidemic at a time when female survivorship improved. These results might indicate greater buffering of females during childhood (and greater sensitivity of males to environmental conditions) before the Black Death; an interaction among improved nutrition, earlier age at menarche, and early growth cessation among females after the Black Death; disproportionate access to dietary resources for males in the aftermath of the epidemic; the disproportionate deaths of frail males during the Black Death; or some combination of these factors.

It is crucial to emphasize that the findings from this and previous studies suggesting improvements in health following the Black Death should not be viewed as evidence that the epidemic was ultimately good for affected populations. Any positive outcomes from the epidemic came at an unimaginably high cost in terms of the numbers of lives lost and the psychosocial stress experienced by survivors. Ideally, research on the context and consequences of the Black Death can allow us to identify factors that promote mortality crises and societal disruption and that potentially can be addressed in living populations (DeWitte, 2016; DeWitte et al., 2016).

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Table 1: Samples sizes from the medieval London cemeteries.

Site	Time Period	Sample Size
Guildhall Yard	Early pre-Black Death	13
St. Mary Spital (Period 14)	Early pre-Black Death	109
St. Nicholas Shambles	Early pre-Black Death	133
St. Mary Spital (Period 15)	Late pre-Black Death	247
St. Mary Graces	Post-Black Death	117
St. Mary Spital (Period 17)	Post-Black Death	212

Table 2: Age-at-death distributions from all periods used in this study (% refers to percentage of total sample for each period that falls in the corresponding age-interval).

Age	Early pre-Black Death	Late pre-Black Death	Post-Black Death
5-14.99	8 (3.2%)	12 (4.858%)	15 (4.62%)
15-24.99	86 (34.4%)	87 (35.222%)	97 (29.85%)
25-34.99	40 (16%)	84 (34.01%)	78 (24%)
35-44.99	45 (18%)	35 (14.17%)	39 (12%)
45-54.99	14 (5.6%)	7 (2.834%)	14 (4.3%)
55-64.99	9 (3.6%)	5 (2.024%)	11 (3.38%)
65-74.99	27 (10.8%)	11 (4.453%)	43 (13.23%)
75+	21 (8.4%)	6 (2.429%)	28 (8.62%)
Total	250	247	325

Table 3: Temporal trends in linear enamel hypoplasia (LEH); percentages of those with and without LEH within each time period are shown in parentheses. P-values are reported for Chi-square tests of differences in presence/absence of LEH between time periods (Early vs. Late pre-Black Death, and Late pre- vs. post-Black Death).

	LEH presence	**Early pre-Black Death**	**Late pre-Black Death**	**Post-Black Death**	**Early vs. late Pre-Black Death *p***	**Late Pre-Black Death vs. post-Black Death *p***
Pooled age/sex	**absent**	36 (36.4%)	37 (28.2%)	68 (42.5%)	0.19	0.012
	present	63 (63.6%)	94 (71.8%)	92 (57.5%)		
Males	**absent**	12 (36.4%)	10 (22.2%)	33 (47.1%)	0.17	0.007
	present	21 (63.6%)	35 (77.8%)	37 (52.9%)		
Females	**absent**	14 (33.3%)	18 (32.7%)	21 (40.4%)	0.95	0.41
	present	28 (66.7%)	37 (67.3%)	31 (59.6%)		

Table 4: Results of T-tests of temporal trends in tibial length. Tibial lengths are provided in mm and the standard deviations are provided in parentheses.

	Early Pre-Black Death	**Late Pre-Black Death**	**Post-Black Death**	**Early vs. Late Pre-Black Death *p***	**Late Pre-Black Death vs. Post-Black Death *p***
Male	369.81 (19.4) n = 32	361.98 (16.9) n = 41	370.94 (21.6) n = 68	0.04	0.001
Female	343.9 (19.9) n = 31	345.78 (23.6) n = 50	340.20 (20.1) n = 54	0.36	0.09

Table 5: Results of Kaplan-Meier survival analysis. Mean survival times (mean ages-at-death) in years are shown with 95% confidence intervals in parentheses.

	Early pre-Black Death	**Late pre-Black Death**	**Post-Black Death**	**Early vs. late Pre-Black Death** ***p***	**Late Pre-Black Death vs. post-Black Death** ***p***
Pooled sex	38.55 (35.88 - 41.22)	31.65 (29.68 - 33.62)	39.58 (37.22 - 41.94)	<0.001	<0.001
Male	42.49 (38.16 - 46.81)	33.92 (31.12 - 36.72)	43.89 (40.59 - 47.18)	<0.001	<0.001
Female	41.73 (37.97 - 45.49)	33.49 (30.49 - 36.50)	39.39 (35.76 - 43.01)	<0.001	0.02