Title: Comparisons of age-at-death distributions among extinct hominins and extant non-human primates indicate normal mortality

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Data availability statement

The data that support the findings of this study are available from published resources as cited within the manuscript and collated on Github https://github.com/claremcfadden/fossil-hominin-mortality.git

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Abstract

Most modern mammalian populations exhibit higher mortality at both ends of the age-at-death distribution. Yet our hominin ancestors reportedly do not exhibit this same distribution, with explanations ranging from predation to taphonomic causes. This paper compares mortality distributions of extant non-human primates to fossil hominins by applying the D0-14/D age-at-death estimation method. Using subadult and adult counts for four extinct hominin taxa, we fitted the hominin data to a modern human mortality curve, resulting in hypothetical mortality distributions. With the expectation that fossil hominin taxa likely fall somewhere on the continuum of non-human primate to human life histories, we compared the distributions to those of five extant catarrhine primate populations. Subadult mortality amongst the extinct hominin groups was typically within the range of that of extant non-human primate groups, and the previously reported high mortality amongst young and middle aged adults in hominin assemblages may be explained by normal, multi-cause deaths.

1 Introduction

Paleodemography is the study of past population dynamics including mortality, fertility, migration, population size and structure. Traditionally, paleodemographic research has focused on archaeological evidence (including radiocarbon dates, settlement size, artefact concentrations, and skeletal remains) relating to *Homo sapiens* from the Neolithic onwards (referred to hereafter as modern humans), with research questions aimed at examining the life history of populations, including major events and transitions (such as the transition to farming) and environmental, social and biological influences and consequences (Chamberlain, 2006). Our interest in the responses of populations to extrinsic and intrinsic stimuli is driven by a desire to understand the nature of humans and human ancestors; our resilience and adaptability in the past, and what this may mean for human populations in the future. One of the best indicators of demographic responses to major events and stimuli is the age-at-death distribution of a population. A typical mammalian age-at-death (or mortality) distribution sees a heightened risk of death for the vulnerable youth (in humans, from birth until approximately 5 years of age) and the elderly, in comparison to the remaining age groups (broadly, older subadults through to middle-aged adults) (Sibly et al., 1997., Robson & Wood, 2008; Bronikowski et al., 2011). Deviations from this structure may serve to tell us about fluctuations in fertility, mortality and growth rates or pressures on any of these variables in a population.

There are a range of factors that may undermine the integrity of the estimated age-at-death structure of a population and may cause erroneous deviations from the expected distribution. Underenumeration (i.e., where a particular demographic or demographics are not accurately represented in a sample, typically the very young and the elderly) is commonly encountered in modern human cemetery contexts resulting in unrepresentative age-at-death distributions (McFadden and Oxenham, 2018). Causes range from poor preservation to differential burial and the impacts of age (young and old) and disease on bone density (Djuric et al., 2011; Gordon

and Buikstra, 1981; Guy et al., 1997; McFadden and Oxenham, 2019; Pokines and Paz, 2016; Walker et al., 1988). A further concern in the analysis of human skeletal remains is the error-prone nature of age-estimation methods for adults, with the error increasing with age (Kemkes-Grottenthaler, 2002; Savall et al., 2016, Wittwer-Backofen et al., 2008). While such concerns are true for modern humans, the gravity of their impacts are undoubtedly far greater for fossil hominins. Fossil evidence for our human ancestors is notoriously difficult to find: the time depth of their lives exposes their skeletal remains to significantly greater taphonomic processes. Interestingly, Surovell et al. (2009) argued that on the one hand taphonomic bias may be expected to increase consistently with increasing age, yet on the other, the increased depth below the surface combined with the perceived value of older archaeological, paleontological and paleoanthropological evidence, may in fact serve to decrease loss of such materials as their age increases. In the context of fossil hominins, we should also consider the overwhelming interest in fossil hominins, which means there are greater resources (financial and human) devoted to locating and excavating them. While taphonomically susceptible, fossil hominins may also experience some preferential conditions when it comes to preservation and sampling, though not to any extent that would entirely counter the deep time impacts on representation. As such, when considering fossil hominin paleodemography we must carefully consider how representative their remains are of the once living populations.

To overcome underrepresentation and bias issues in skeletal samples of modern human populations, methods have been developed to predict population dynamics using commonly available and less error-susceptible sources of data. The proportion (sometimes incorrectly described as a ratio) of subadults, for which age can be estimated with accuracy and precision, in a population should be heavily influenced by and therefore predictive of the fertility rate of the population (Corruccini et al., 1989; Johansson and Horowitz, 1986; Konigsberg and Frankenberg, 1994; Sattenspiel and Harpending, 1983). Various methods have been developed

on this basis (Bocquet-Appel, 2002; Bocquet-Appel, 2011; Bocquet-Appel and Masset, 1982; Buikstra et al., 1986), with one recent iteration being the McFadden & Oxenham (2017) D0-14/D method. The D0-14/D method uses the number of individuals aged 0-14 years divided by the total number of deaths in the sample as a proxy for the estimation of fertility and the rate of natural population increase when infants are well-represented (McFadden & Oxenham, 2017; 2018). The use of the D0-14/D method has been extended to estimating the age-at-death distribution (McFadden, Cave & Oxenham 2019). This is a valid endeavor because the D0-14/D proportion is a proxy for fertility, which significantly influences the age-at-death distribution of a population (Corruccini et al., 1989; Johansson and Horowitz, 1986; Konigsberg and Frankenberg, 1994; Sattenspiel and Harpending, 1983). The D0-14/D method can be applied to small samples, can accommodate imprecise age estimates (requiring only the number of subadults and total number of individuals in the sample), and has been proven to be a relatively stable measure even with some degree of under-enumeration of the infants and elderly (McFadden & Oxenham, 2019 for analyses of the degree of under-enumeration that can be accommodated by the method for different age groups).

Past paleodemographic analyses of Neanderthals and earlier hominins such as *Australopithecus* spp. and *Paranthropus* spp. have been sparingly undertaken, in large part due to data unavailability (McKinley, 1971; Mann, 1975; Trinkaus, 1995, Bocquet-Appel & Arsuaga, 1999, Bermúdez de Castro et al. 2004; Caspari & Lee, 2004). However, even based on limited research, an interesting and unexpected picture of past hominin mortality has emerged. More specifically, when paleodemographic estimation methods are applied to extinct hominin samples, they have produced mortality distributions suggesting reproductive adults, or "prime adults", were the most vulnerable age group (McKinley, 1971, Bocquet-Appel & Arsuaga, 1999; Bermúdez de Castro et al., 2004). For example, it has been reported that *Australopithecus africanus* and *Paranthropus robustus* experienced the greatest mortality risk during adulthood

(McKinley, 1971). By contrast, studies of Middle Pleistocene hominins suggest the most vulnerable age group was 11-20 years of age, during their juvenile years and early adulthood (Bocquet-Appel & Arsuaga, 1999; Bermúdez de Castro et al., 2004). Several explanations for these unusual mortality observations have been proposed, including that predator cave deposits may represent only a subset of the hominin population (e.g., bears targeting roaming hunters who are more likely to be "prime adults"), or that old and young individuals are removed from the fossil record through high mobility induced attrition (Bocquet-Appel & Arsuaga., 1999; Bermúdez de Castro et al., 2004).

In contrast, when deviations from the expected age-at-death distribution are observed in *Homo sapiens* populations, particularly those belonging to the Holocene, we often have sufficient contextual information to determine whether they are caused by unusual population dynamics (such as mass mortality events) or are the result of introduced bias (such as poor preservation). This is frequently achieved through cross-referencing mortality distributions with other sources, such as historical accounts of plague and famine (e.g., Geber, 2016; DeWitte, 2014), inferences of differential mortuary practices for certain demographics (e.g., literature review by Betsinger & DeWitte, 2021), paleopathological and trauma evidence indicative of disease or warfare (e.g., Ham et al., 2021; Steadman, 2008), or analysis of taphonomic conditions. Importantly, as we can observe the typical mortality distribution of *Homo sapiens* it is far easier to identify and evaluate deviations. Many of the supplementary sources of information that may contextualize unusual mortality distributions in human populations are absent or obscured for fossil hominins. Therefore, we argue that one avenue of investigation is further examination and comparison of the mortality distributions themselves and the methodologies that influence them.

In this paper, we apply the D0-14/D method for estimating the components of the age-at-death distribution to four fossil hominin samples. As previously noted, the D0-14/D proportion has

good robusticity for such applications as it can handle small samples, is relatively impervious to uncertain age estimates, and it can accommodate to some extent the impacts of underenumeration through taphonomic or other causes (see McFadden et al., 2019). The method essentially fits age-at-death data to a modern human mortality curve, based on the proportion of subadults in a sample and the way this influences the remaining shape of the curve (see McFadden & Oxenham, 2017 and McFadden et al., 2019 for further discussion).

Using this method, we seek to evaluate and compare the mortality distributions of fossil hominins to those of extant non-human primates as an exploratory exercise. In theory, if all extinct and extant primate taxa show a similar mortality profile, this may suggest that fossil hominin assemblages are not the result of predation, catastrophic mortality, or major taphonomic bias, but rather indicate nuanced differences in life history patterns between taxa. In contrast, if there is a great degree of heterogeneity amongst taxa, particularly between the extinct and extant groups, then we may either be observing greater differences in life history patterns, unusual mortality distributions in some samples, or the effects of age-estimation and mortality distribution modelling.

2 Materials and Methods

2.1 Dataset composition

The extant primate dataset consists of five catarrhine taxa, *Cercopithecus mitis* (blue monkey), *Papio cynocephalus (yellow baboon)*, *Pan troglodytes* (chimpanzee), *Pongo abelii* (Sumatran orangutan), and *Gorilla beringei* (Eastern gorilla) (Table 1), represented by five discrete samples. Age-at-death information for four of these taxa (*C. mitis*, *P. cynocephalus, P. troglodtyes, and G. beringei*) were obtained from Bronikowski et al.'s (2016) database covering 30 years of wild primate surveys. For the majority of individuals within each sample, the ages at death were known to within a single year, with the exception of individuals that

were present at the commencement of each study where the age was estimated based on physical characteristics (Bronikowski et al., 2016). Annual death rates including age-at-death data of wild Sumatran orangutans (*P. abelii*) were obtained from Wich et al. (2004) (n=23), who reported the life history of wild orangutans in the Gunung Leuser National Park, Leuser Ecosystem, Sumatra, Indonesia, from a 32- year research project. None of these samples are pooled; they represent true populations.

<Table 1. Description of samples>

The fossil hominin datasets include a Middle Pleistocene *Homo* sample from Sima de los Huesos, and samples of *Homo neanderthalensis*, *Australopithecus africanus* and *Paranthropus robustus* (Table 1). The pooled Neanderthal data is a collection of skeletal remains representing 206 individuals from Middle Pleistocene Europe and Asia (Trinkaus, 1995) dated to between 100 and 35 thousand years ago. The sample data for earlier hominins *A. africanus* (n = 65) dated to between 3.3 and 2.1 million years ago and *P. robustus* (alternatively referred to as *Australopithecus robustus*) (n = 143) dated between 1.8 and 1.2 million years ago were extracted from McKinley (1971). The Sima de los Huesos sample, dated to 430,000 years ago (Arsuaga et al. 2014), represents an early Neanderthal population (Meyer et al. 2016) and is comprised of approximately 29 individuals (Bermúdez de Castro et al., 2020). The age-at-death data for each extinct hominin taxon were obtained using age estimates of previous authors. For the pooled Neanderthal samples, individual specimens were assigned to one of six categories based on the work of Trinkaus (1995); Neonate (fetal to <1 year), Child (1 year to <5 years), Juvenile (5 to <10), Adolescent (10 to <20 years), Young Adult (20 to <40 years) and Old Adult (40+ years). The methods of age determination for the *Australopithecus* and *Paranthropus* samples are described by Mann (1968) who applied a tooth eruption and wear method and categorized them into individual and relative ages, McKinley (1971) then redistributed each individual into five-year categories, 1-5 years, 6-10 years, 11-15 years, 16-

20 years, 21-25 years, 26-30 years, 31-35 years and 36-40 years. For the Sima de los Huesos sample, Bermúdez de Castro et al. (2004) estimated juvenile age-at death using dental development, while adults were aged based on dental wear. A subsequent analysis by Bermúdez de Castro et al. (2020) reported an increase in the minimum number of individuals from 28 to 29. The number of immature individuals was reported to be 13 (Bermúdez de Castro et al., 2020).

The *H. neanderthalensis*, *A. africanus* and *P. robustus* samples can be considered pooled temporally, geographically or both. While this pooling undoubtedly imposes epistemological and interpretive implications upon the results, it does not necessarily undermine them. In the majority of paleodemographic studies of modern humans, the aim is to examine how a specific population responds to specific stimuli. Demographic fluctuations (at least those which are commonly of interest to researchers) typically occur over years, decades or potentially hundreds of years, but due to the self-regulating nature of populations these fluctuations are generally smoothed out when we examine them across millennia (Boone, 2002). As such, to understand demographic fluctuations in the past, most paleodemographic research requires a substantial degree of temporal and geographic precision, as well as two or more datapoints from which to evaluate the response (e.g., before and after an event). Additionally, these types of research questions are reliant on our concept of a population as a temporally and geographically constrained, cohesive unit, as it is the population itself that is of interest.

In our application of paleodemographic analysis in this paper, we pursue an alternative aim of evaluating typical mortality profiles for taxa (not discrete populations), which makes no less substantial contribution to our understanding of extinct hominin populations yet avoids the need for the sort of temporospatial precision outlined above. Importantly, the pooled samples are treated as representative of taxa rather than discrete populations, with the aim being to identify whether the typical age-at-death distribution of each taxon remains anomalous (as

previous studies have identified) or whether it conforms to the expected mammalian distribution when the D0-14/D age-at-death distribution method is applied. Indeed, the averaging effect of pooling geographically and temporally discrete samples is advantageous for this outcome, as observing a single population would increase the susceptibility to context-specific demographic influences (e.g., effects of predation, high mobility, etc.) and thus atypical population structures. For the sake of clarity, we do not seek to identify demographic fluctuations as is typical of modern paleodemographic research; we acknowledge the inability to do this with the currently available fossil hominin data. Instead, we seek to average the population dynamics across pooled samples to learn something of the typical demographic structure of extinct taxa. Notwithstanding, if there are consistent biases throughout the collective fossil record, the resulting pooled sample will reflect these. If this is the case, such biases should be identifiable through the comparison of mortality distributions with those of extant primate taxa, and potentially with those of other, better-represented fossil hominins.

2.2 Data standardization

The subadult to adult cut off for the D0-14/D method assumes sexual maturity in humans at a mean age of 15 years for both males and females (Beunen, Rogol & Malina, 2006). In the context of the current study, and as estimating sexual maturity for fossil hominin taxa is not possible, we assessed subadult/adult cut-off ages using dental maturity. This is a marker of maturity that is easily and objectively quantified (Balolia et al., 2013) and acts as a uniform marker of maturity across extant primate and fossil hominin samples alike. This method divides subadults and adults based on whether the upper and lower third molars have fully erupted (Miles, 1963; Holly Smith, Crummett & Brandt, 1994; Balolia, Soligo & Lockwood, 2013). The age of dental maturity has been well established in many primate species (Holly Smith, Crummett & Brandt, 1994; Anemone, Watts & Swindler, 1991; Dirks & Bowman, 2007). Accordingly, we used published M3 eruption ages to divide each non-human primate

species into subadults and adults (Table 1). As the *H. neanderthalensis*, *A. africanus* and *P. robustus* samples were originally separated into five- or ten-year age categories, we assigned a subadult age of <15 years for all samples. Based on M3 eruption ages of non-human primates it is unlikely that dental maturity would have considerably exceeded 15 years of age in Middle Pleistocene *Homo* and earlier hominins (Smith, 1991; Smith et al., 2007; 2010). We take this approach to provide a basis for separating pre-determined age brackets whereby the original material was not available for assessment of M3 eruption. In the case of an age bracket overlapping with the 15 years cut-off, the younger category was determined as subadult whilst the older as adults. For example, within the pooled *H. neanderthalensis* sample all individuals within the juvenile category (5 <10 years) were classified as subadults whilst those in the adolescent category (10 < 20 years) as adults. This was decided as individuals over 15 years would likely have experienced dental maturity thus their inclusion in the subadult category would provide less reliable results. For Sima de los Huesos, immature individuals were defined by Bermúdez de Castro et al. (2020) as those without erupted M3 and, in accordance with this and the definition applied to other fossil hominins in this study, we considered them to be subadults (D0-14) in this analysis.

2.3 Application of the D0-14/D Method to Fossil Hominins

Once data were standardized and appropriate subadult to adult demarcations determined, we calculated the D0-14/D proportion (i.e., the number of individuals who have not reached dental maturity divided by the total number of individuals in the sample) for each fossil hominin sample. We subsequently used McFadden et al.'s (2019) regression equations (Table 1, p.1074) for distributing individuals that had attained dental maturity into discrete age categories to create an estimated mortality profile. This method estimates the percentage of individuals that might be expected to die in each of 10 age categories (15-34 years, 35-39 years, and so on to 75+ years) that are relevant in modern human populations, however, these categories are not

relevant to all taxa in the current study. As such, to allow comparison across taxa that display differences in life expectancy, the age categories were converted to maturation phases (Phase 1 being equivalent to *Homo sapiens* 15-34 years, Phase 2 being equivalent to 35-39 years, and so on). The percentages of individuals in each maturation phase were then multiplied by the total number of individuals in the sample that had attained dental maturity, to give a number of individuals for each phase. These numbers were then rounded to integers and converted back to proportions of the total sample, so that each maturation phase represented a whole number of individuals.

In applying the method to fossil hominins, we do not suppose that they share the same mortality curve as modern humans. Under the assumption that fossil hominin mortality distributions likely fall somewhere on the continuum of non-human primates to humans, we compare hypothetical distributions where fossil hominin mortality does resemble that of modern humans, with the actual mortality distributions of extant non-human primates. In doing so, we can observe mortality under modern human life history conditions, identify whether the hypothetical fossil hominin distributions show strong deviances from those of extant non-human primates, and explore the similarities or differences in the mortality distributions of all included primate taxa. As age estimates of this specificity have not previously been made for fossil hominins, we did not make formal comparisons between previous mortality distributions and those estimated here. However, in discussing our results we do draw qualitative comparisons between previously published descriptions of fossil hominin mortality profiles and our estimated hypothetical distributions. As the fossil hominin distributions were estimated using the procedure (McFadden et al., 2019), comparisons were not made among fossil hominin taxa, but rather between fossil hominins and extant primates.

2.4 Standardizing Extant Primate Age-at-Death Data across Maturation Phases

To allow comparisons between fossil hominins and extant primates, all of which have varying

lifespans, it was necessary to also standardize the extant primate data. This was performed for fossil hominins as part of the McFadden et al. (2019) estimation procedure. In contrast, for the extant non-human primate samples for which actual age-at-death data were available, the ages corresponding to each phase were identified by dividing the lower (except for this first phase, where the lower limit is defined by dental maturity) and upper limits of the phase by the final age phase (75+ years, as the original method is based on *Homo sapiens*), then multiplying this by the maximum age in the sample. Where the resulting demarcation was less than 0.5 of a year, the demarcation was set below that year, and where it was above 0.5 it was set at that year (for example, 32.26 would be a cut off of 31 years to reflect those aged <32 years, and 35.93 would be cut off at 35 to reflect those aged <36 years). For *P. cynocephalus*, as an example, the oldest age observed in the sample was 27 years. For Phase 1 (15-34 years in humans), the ages corresponding to the phase were determined by the lower limit of dental maturity being 8 years of age, and the upper limit was determined by multiplying 27 years by 0.45 (34 years divided by 75 years, based on the modern human distribution), giving Phase 1 an age range of 8-11 years. This means the age-at-death data for the extant primates are condensed into maturation phases (for the purpose of comparability and standardization), but are not estimated in the same way fossil hominin distributions are.

2.5 Comparison of Mortality Distributions

The accuracy of McFadden, Cave and Oxenham's (2019) age-at-death distribution estimation method which uses the D0-14/D proportion to distribute individuals into age categories has been shown to be valid for modern human populations but has not yet been applied to non-human populations. In this study, we apply the D0-14/D calculation and the associated age-at-death estimation procedure to four fossil hominin samples to produce hypothetical mortality distributions, in which fossil hominin mortality hypothetically follows a similar pattern to modern human mortality. As previously noted, we are not testing the hypothesis that fossil

hominin mortality follows the same distribution as that of modern humans (as we do not have a means of validating this). Instead, this is an exploratory exercise to identify consistencies and inconsistencies between the modern human model of fossil hominin mortality and actual age-at-death distributions for extant non-human primates. Based on these observations, it is likely that any similarities observed between the two estimates indicate consistencies in the mortality profiles of all primates (Bronikowski et al., 2011) and potentially even most mammals (Schindler et al., 2012). This may lend support to the fossil hominin samples being representative of the life history of their taxa, and similarities among extinct and extant taxa may reveal some information about their life histories. By contrast, dissimilarities indicate heterogeneity in the mortality distributions of primates or between extinct and extant primates. Such patterns may support the suggestion that extinct fossil taxa show unusual mortality distributions, driven by taphonomy or specific mortality conditions (such as predation). Alternatively, it may indicate some effect of the age-at-death modelling procedure (which will create some artificial consistencies between fossil hominin distributions as a result of the model calculation).

In our study, subadults are the only group for which age is known with some confidence for all samples, including extant and extinct taxa. For all other age groups, age is confidently known for the extant taxa but is estimated for the extinct taxa. As such, subadults were the only age group that we could reasonably examine the likelihood of underrepresentation in by using actual (rather than estimated) counts. In modern humans, underrepresentation of subadults (if not the result of differential burial based on chronological or social age; or other cultural aspects such as whether the child was baptized or not) is often argued to be due to taphonomic processes resulting in the loss of small and often low density subadult skeletal remains (Djuric et al., 2011; Gordon and Buikstra, 1981; Guy et al., 1997; Pokines and Paz, 2016), the impacts

of which may well extend to fossil hominin subadults. To test this, we analyzed the number of subadults and adults for each taxon using a chi-square contingency table.

To quantitatively compare the distributions of each taxon, principal component analysis (PCA) was used to identify any major components that may indicate homogeneity in some aspect of mortality among the included taxa. Additionally, it was used to examine component loadings among taxa, to identify if any particular taxon or group of taxa exhibited deviations from the others. PCA was calculated based on the number of individuals in each maturation phase (rows) for each sample (columns). Further descriptive statistics (mean and standard deviation) were calculated based on the results of the PCA. Mortality distributions based on the maturation phases were plotted as a bar graph for visual comparison. Notably, both the PCA and bar chart were considered exploratory exercises to look for consistencies and disparities between extant and extinct primates. All statistics were performed in SPSS v.27 (IBM Corp, 2020).

3 Results

The chi-square contingency table found that the *P. cynocephalus*, *H. neanderthalensis* and *A. africanus* samples deviated most from the expected counts for both subadults and adults (Table 2). The *P. cynocephalus* sample had more subadults and less adults than expected, while the *H. neanderthalensis* and *A. africanus* samples showed the reverse trend. All other taxa exhibited low chi-square values, suggesting good agreement between the observed and expected counts for subadults and adults. These results indicate that there is potentially some bias in the *H. neanderthalensis* and *A. africanus* samples in the form of subadult underrepresentation, if we expect these taxa to have similar life history patterns to the other taxa represented.

<Table 2. Chi square contingency table for subadult and adult representation>

The principal component analysis (PCA) identified that PC1 accounts for a very high proportion (91%, eigenvalue 8.22) of the variance (Table 3). Examining the coefficients for each taxon (Table 4), remarkably similar loadings were found across extinct fossil hominin and extant non-primate groups. As shown in Table 5, the mean value for PC1 across all taxa was -0.33 with a standard deviation of just 0.02. These values remained consistent even when performed on the extinct and extant taxa separately. This suggests that PC1 represents similarities in the nature and shape of the mortality distributions for all taxa included in the analysis. As no single sample (nor grouping of samples) deviated from this, it appears that all taxa have a somewhat typical mortality distribution; that is, there is no evidence to suggest that any samples experienced an unusual mortality distribution in comparison to the others.

<Table 3. PCA eigenvalues, proportions and cumulative proportions>

<Table 4. PCA loadings by taxa and component>

<Table 5. Means and standard deviations for component loadings>

<Table 6. PCA correlation matrix>

PC2 of the model, accounting for 6% of the variance (eigenvalue 0.55) (Table 3), was the only PC for which the extant and extinct taxa loadings collectively occurred in opposite directions (positive for extant, negative for extinct) (Table 4). While this only accounts for a small amount of the variance, it is nonetheless informative as it clearly separates the two groups. The mean for the extinct taxa was -0.33 with a standard deviation of 0.26, indicating reasonable heterogeneity among the fossil hominins. Further components were not explored due to the very marginal explanatory power (<2%) and lack of patterns in taxon loadings. The mortality distributions of the taxa are visualized in Figure 1 and the distributions for individual taxa can be found in the Appendix.

As may be expected due to the commonality of the age-at-death distribution estimation procedure, the fossil hominins exhibit close correlations (Table 6, range r=0.855-0.999). However, more interesting are the strong correlations between *H. neanderthalensis*, *P. robustus*, and the Sima de los Huesos samples with all extant primates except *P. abelii* (Table 6, range r=0.874-0.982).

<Figure 1. Bar chart of mortality distributions for five extant non-human primate and four fossil hominin samples>

4 Discussion

The findings of the chi-square contingency table, principal components analysis (PCA), and visual inspection of the plotted data are not indicative of consistently major underenumeration of subadults across these taxa. The *H. neanderthalensis* and *A. africanus* samples appear to show some underenumeration of subadults. This could be the result of the loss of subadult remains through taphonomic processes, attritional mortality in highly mobile groups, lower fertility rates in these taxa (e.g., for *H. neanderthalensis* see discussions by Churchill (2014), Sørensen (2011) and Nakahashi et al. (2018)), or differing overall life history patterns. However, the degree of underenumeration and deviation of subadult proportions does not have seem to have a substantial effect on the overall distribution based on the PCA results. The PCA demonstrated that a single component accounted for 91% of the variance, and individual taxon loadings are consistent in all cases, suggesting that the nature of the mortality profiles among the included taxa (both extant and extinct) are similar. Thus, while subadults may show some variable representation among taxa, the overall mortality distributions appear to be representative and reasonably consistent across all samples in this study. The correlation matrix was generally supportive of this, though some taxa showed deviations from others. The second component, and the only other component of any explanatory power, is a factor dividing the extinct from extant non-human primates. Though this factor only accounted for 6% of the

variance, no other factor divided the two groups. What this factor represents is unclear, but the variation of its loading within the extinct and extant groups when separately examined suggests it is not necessarily a result of the D0-14/D age-at-death distribution method used in this study, or we would expect to see greater homogeneity among the fossil hominins.

Contextualizing these findings with our understanding of primate ecology helps to explain the consistencies and variation among taxa in mortality distributions. The known mortality distributions for *P. troglodytes* in this study are consistent with the literature, particularly in relation to the high mortality rate in subadults and middle-aged adults (Hill et al., 2001; Muller & Wrangham, 2014; Thompson et al., 2020; Williams et al., 2008). These age-specific death rates vary between populations and are believed to have resulted from biological and ecological factors (Hill et al., 2001; Hawkes, 2010; Muller & Wrangham, 2014; Thompson et al., 2020). Several variables have been proposed that influence subadult and middle-aged death rates including smaller body size and slower growth rates compared to other hominoids, intraspecific aggression and violence, predation, and in extreme cases, catastrophic events like habitat loss or disease (Hill et al., 2001; Kuehl et al., 2008; Muller & Wrangham, 2014; Wrangham et al., 2006; Williams et al., 2008). Elderly chimpanzees show significant declines in physical conditions with age resulting in frailty and respiratory illness (Thompson et al., 2020). In contrast, *G. beringei* are considerably larger in body size and due to the relatively low frequency of intrasexual aggression, adults typically have low rates of mortality compared to humans and chimpanzees, which is reflected in the predicted mortality distribution (Harcourt & Stewart, 2007). The mortality distribution of *P. abelii*, who show higher adult death rates compared to subadults, differs from the pattern found in the other great apes. *P. abelii* differ in life history patterns compared to other great apes as they have lower fertility and longer inter-birth intervals and have very low mortality rates in general, therefore the observed mortality distribution is not surprising (van Noordwijk et al., 2018; Wich et al., 2004). Moreover, the

high mortality rate in mid-adults could be due to intense and aggressive male competition and risks associated with male takeovers observed in orangutans (Utami et al., 2002; Balolia et al., 2017). While the extant non-human primate samples analyzed span narrower temporal and geographic limits than the fossil hominin samples, they are considered to be representative of their taxa to a substantial degree. In addition to the distributions matching well with what we know of primate ecology, the results of the chi-square and PCA analyses are also in support of this.

Modelling the age-at-death distributions of fossil hominins using a *Homo sapiens* mortality curve has allowed us to examine consistencies and deviations among taxa. While the overall shape of the curve has proven to be relatively homogenous among groups (consistent with previous reports by Bronikowski et al., 2011 and Schindler et al., 2012), the modern human model infers a greater proportion of deaths in older maturation phases than observed in any of the extant non-human primates. It therefore seems unlikely that this is a true representation of the age-at-death distribution of fossil hominin taxa respectively. If the fossil hominins were to have a greater proportion of deaths in the young and middle maturation phases, as has been reported in previous fossil hominin demographic studies, and a smaller proportion in the older maturation phases, their distributions would correspond closely with the likes of the *P. abelii* and *P. troglodytes* populations. The high proportion of individuals represented in the young and middle maturation phases of the age-at-death distribution for both extant species are indicative of high-risk activities, as previously discussed, such as hunting behaviors leading to accidental death or increased predation, which may be true too of the fossil hominin taxa. These activities and associated multi-causal mortality have previously been proposed and are well discussed for *H. neanderthalensis* (Gat, 1999; Pettitt, 2000; Zollikofer et al.; 2002; Camarós et al., 2016; White et al., 2016; Gaudzinski-Windheuser et al., 2018).

Extending this to other taxa, some populations of *P. troglodytes* located in Tanzania inhabit more open woodlands and are potentially more vulnerable to predators, similar to the environment previously proposed for *P. robustus* (Badenhorst, 2018, Codron et al., 2008, Crook & Gartlan, 1966, Ogawa & Kanamori, 1999, Pruetz et al., 2008, Tsukahara, 1993). Moreover, in a wild population of *P. troglodytes* located in Gombe National Park, the highest proportion of adult death was reportedly due to illness, specifically respiratory diseases (Williams et al; 2008). The same study also demonstrated that lethal intraspecific aggression between neighboring communities was the greatest cause of death for middle aged adult males (20-30 years) (Williams et al; 2008). Similar intraspecific aggression between mature adult males has previously been proposed for *P. robustus* which, in conjunction with high predation rates, highlights an evolutionary trade-off (Lockwood et al; 2007). Therefore, adult paranthropines may have been under similar risks of mortality as modern chimpanzees, i.e., predation, competition and disease, which was potentially escalated due to living in an open savanna environment.

Evidence of predation on *A. africanus* has been previously reported with respect to predatory birds (Berger, 2006; Berger & McGraw, 2007). Accumulations of modern primate bones, discovered in nests of the modern African crowned eagles, demonstrate catastrophic mortality patterns (McGraw, Cooke & Shultz, 2006; Sanders, Trapani & Mitani, 2003). However, the hypothetical modelling of *A. africanus* in this study did not identify this taxon as a particular outlier. The pooled sample shows some evidence of subadult underenumeration, and the results of the PCA suggest it is unusual with regards to PC2 (the factor dividing the extant and extinct taxa), exhibiting the highest negative loading within the fossil hominins by some magnitude. As such, the results of the *A. africanus* hypothetical mortality modelling are inconclusive, but indicative of some differential conditions effecting fertility, mortality or representation.

For the Sima de los Huesos sample, our results suggest overall subadult mortality and representation is well within the range of other fossil hominins and extant non-human primates. Though we agree with Bermúdez de Castro et al. (2020) that the near absence of younger children altogether is unusual, it is possible that with such a small sample size it is only a very small number (1-2) of young children missing from the sample (or 3-4 subadults total based on the chi-square results). If the Sima de los Huesos sample was to include a greater number of young children, it would align more closely with extant non-human primate distributions, such as those of *C. mitis*, *G. beringei* and *P. cynocephalus*. There is no evidence to suggest that one of these outcomes is more likely than the other and therefore they should be considered equal possibilities. However, it is interesting that the results indicate the Sima de los Huesos mortality distribution is not particularly unusual when compared to the taxa analysed in this study. If the Sima de los Huesos assemblage is indeed a predatory accumulation, based on the findings of this study it seems that it is a somewhat randomly selected one. Further, if the Sima de los Huesos assemblage does have a relatively typical mortality distribution, as is possible based on the chi-square (indeed, this sample had the second lowest chi-square value) and PCA results, then this may lend support the claim by Carbonell and Mosquera (2006) that the assemblage represents intentional burial, as we would expect to see a normal mortality distribution in typical burial conditions. As this study has only modelled the mortality distribution, further evidence would be necessary to validate this inference.

Finally, the fertility implications of these findings should be considered in future research. Though it is not possible to explore this within the scope of this paper, the similarities and differences in subadult representation across taxa are indicative of corresponding variation in fertility rates (Corruccini et al., 1989; Johansson and Horowitz, 1986; Konigsberg and Frankenberg, 1994; McFadden & Oxenham, 2017; Sattenspiel and Harpending, 1983). This is an additional, and equally important, potential application of the D0-14/D proportion and

associated fertility estimator (McFadden & Oxenham, 2017). Based on the visual representation of the data in this study, it appears that fertility among the fossil hominin taxa ranges from similarities with the known low-fertility *P. abelii*, to higher fertility primates such as *P. troglodytes*. These findings should be explored further both quantitatively and qualitatively in the context of known life history patterns for extant non-human primates.

5 Conclusion

Previous research has shown unusual mortality distributions for fossil hominin samples. We modelled mortality distributions for *P. robustus*, *A. africanus*, *H. neanderthalensis* and a Middle Pleistocene *Homo* sample from Sima de los Huesos using the D0-14/D method (McFadden et al., 2019). Comparing these hypothetical mortality distributions with those of extant non-human primates, we find that the modern human mortality curve likely overestimates the number of deaths at older ages and underestimates those in young to middle age groups. Notwithstanding, the method produces mortality distributions that are overall relatively consistent with those of extant non-human primates. Furthermore, there are no significant outliers among the estimated mortality distributions for the fossil hominin taxa.

Elevated mortality in the young and middle-aged adult portion of the extant non-human primates is consistent with previous research suggesting high risk behaviors for these species. We suggest that fossil hominins likely experienced similar risks as a natural part of their life course, and that their mortality distributions likely fall somewhere between the hypothetical modern human models presented here and the extant non-human primate distributions. Of particular note, we did not find any evidence to support the Sima de los Huesos assemblage presenting with an unusual mortality profile. While the lack of young children in the sample is unusual, based on our analyses it would seem the number that could be expected to be missing is very low, and would not substantially change the overall mortality distribution. However, as

this is an exploratory exercise in modelling age-at-death distributions, these findings are inconclusive at this stage and require further investigation.

The research presented here indicates that the D0-14/D age-at-death distribution method is a viable way of exploring mortality patterns in fossil hominin populations. Application of this approach to fossil hominin assemblages can accommodate the impacts of commonly observed infant and elderly underenumeration in samples, and uncertain age estimation in fossil hominins. While the results here do not alone support the conformity of fossil hominin populations to mammalian mortality patterns, incorporating a comparative and strongly ecologically contextualized approach with paleodemographic methods such as the D0-14/D method may permit more detailed and nuanced reconstructions of selective pressures facing extinct hominin groups than have previously been possible.

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8 Appendix