Comparative perspective on antemortem tooth loss in Neandertals

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ABSTRACT

Neandertal specimens with severe antemortem (before death) tooth loss (AMTL) are sometimes interpreted as evidence for human-like behaviors, such as conspecific care or cooking, although it is uncertain whether AMTL frequencies in Neandertals are similar to those in modern humans and exceed those in non-human primates. This study characterizes AMTL (all tooth types) in Neandertals relative to recent human hunter-gatherers and several non-human primate taxa using binomial-normal regression models fit in a Bayesian framework to a sample of 25 Neandertals, 310 recent human hunter-gatherers, 61 chimpanzees, 38 orangutans, and 75 baboons. The probability that a tooth is lost antemortem is modeled to depend on tooth class, taxon, and estimated age at death.

Neandertals have odds of AMTL above orangutans and baboons, similar to or somewhat lower than chimpanzees, and below recent humans, if we assume a human-like rate of senescence; or intermediate between chimpanzees and recent humans, if we assume a faster rate of senescence. These findings suggest that Neandertals can only be considered to have frequencies of AMTL above non-human primates if they had more rapid life histories than modern humans. Either Neandertals are not human-like in their life history or their frequency of AMTL.

These interpretations are complicated, however, by the substantial inter-population variation in AMTL among recent humans, with some populations having odds of AMTL as low as in non-human primates. These results, together with theoretical considerations, suggest that only high frequencies of AMTL are diagnostic of behavior. Consequently, the behavioral implications of low frequencies of AMTL, such as those found in Neandertals, are ambiguous. Low frequencies in Neandertals could be because they had a low risk of AMTL rather than

because they had high mortality from AMTL relative to an average modern human of similar age.

Introduction

Neandertals (*Homo neanderthalensis*) are a group of fossil hominins from the Pleistocene of Eurasia that along with “Denisovans” are the closest known relatives of our own, modern human (*Homo sapiens*) lineage (Prüfer et al., 2013). Although “Classic Neandertal” specimens derive from the Late Pleistocene, certain European Middle Pleistocene individuals exhibit Neandertal features that is generally taken as evidence that the Neandertal lineage had deep roots in the Middle Pleistocene (Hublin, 2009; Arsuaga et al., 2014). Looked at from this perspective, Middle Pleistocene “pre-Neandertal” and Classic Neandertal specimens could all be considered to be part of a Neandertal evolutionary lineage, which originated < 500,000 years ago and was centered geographically in Europe. Given the phylogenetic closeness between Neandertals and modern humans, identifying similarities and differences between the two groups in biology and behavior has the potential to provide important insights into what it means to be human.

One category of evidence that is frequently discussed in this context is the presence of several disabled Neandertal or pre-Neandertal individuals (e.g., Aubesier 11 [Lebel et al., 2001; De Gusta, 2003], Shanidar 1 [Trinkaus and Zimmerman, 1982], and Sima de los Huesos 14 [Gracia et al., 2009]), because the survival of these individuals may provide evidence that Neandertals assisted their conspecifics (Solecki, 1960 ; Jolly and Plog, 1982; Trinkaus and Zimmerman, 1982; Tappen, 1985; Dettwyler, 1991; Lebel et al., 2001; Lordkipanidze et al., 2005). For example, Shanidar 1 survived multiple disabling pathologies for a number of years, including a functional amputation of the right forearm, cranial fractures, and advanced degenerative joint disease (Trinkaus and Zimmerman, 1982). Recent discoveries, particularly of Aubesier 11 and Dmanisi D3444/3900 (Lebel et al., 2001 and Lordkipanidze et al., 2005), have

renewed the focus on the role of antemortem (before death) tooth loss (AMTL) in these discussions.

At least three Classic Neandertals appear to have survived the antemortem loss of a significant portion of their dentition. The Guattari 1 maxilla is reported to be completely edentulous (Sergi et al., 1972), La Chapelle-aux-Saints 1 is estimated to have lost 48.3–51.7% of its teeth antemortem (Trinkaus, 1983, 1985), and the Riparo Mezzena partial mandible lost 80–90% of its teeth antemortem in the preserved region (Condemi et al., 2012). There are also several Neandertal specimens with less severe AMTL, ranging from 6.3% to 25% of the teeth lost before death: Shanidar 4 and 5 lost two and three teeth before death, respectively (Trinkaus, 1983); Artenac 1 likely lost the right maxillary canine and central incisor before death (Mann et al., 2007); Krapina 59 shows evidence of the mandibular left third premolar being lost antemortem (Radović et al., 1988); and Guattari 2 lost the right mandibular first molar antemortem, along with showing evidence of more widespread periodontal disease (Mallegni, 1995). It is worthwhile to note that the impact of tooth loss on survival/behavior could vary by tooth type. Wear patterns suggest that tooth type usage can vary with diet and cultural practices (Molnar, 1971).

On the one hand, masticatory impairment and subsequent fitness consequences are inferred for individuals missing a significant portion of their total dentition, prompting researchers to provide an explanation for the survival of these individuals. Jolly and Plog (1982) suggested that the La Chapelle-aux-Saints 1 had conspecifics who specially prepared his food by cutting or pre-chewing it. Brace (1979) took a different approach, arguing that perhaps it was the advent of cooking technology that allowed La Chapelle-aux-Saints 1 to survive. The more recent discoveries of the Middle Pleistocene Aubesier 11 (Lebel et al., 2001; Lebel and Trinkaus, 2002)

and the Early Pleistocene Dmanisi D3444/D3900 (Lordkipanidze et al., 2005; Lordkipanidze et al., 2006) fossils, which are missing significant numbers of teeth, potentially extend these behavioral arguments to as far back as ~1.8 million years ago. Lebel et al. (2001) and Lordkipanidze et al. (2005) cite a variety of potential behaviors to explain the survival of these individuals, including more extensive cooking and preparation of foods, conspecific assistance, or the selection of softer foods; in each case emphasizing the novelty of these behaviors in comparison with non-human primates.

On the other hand, there is abundant evidence that non-human primates can survive significant masticatory impairment, at least occasionally, without practicing any of these behaviors to the extent that modern humans do (Kilgore, 1989; Lovell, 1990; Cuzzo and Sauther, 2004; Struhsaker et al., 2011; Turner et al., 2014). Nevertheless, it does not necessarily follow from these observations that non-human primates survive severe AMTL as *frequently* as modern humans, which is the underlying theoretical premise of associations between AMTL and uniquely human behaviors. Recent results comparing AMTL in recent human hunter-gatherers, chimpanzees (*Pan troglodytes*), orangutans (*Pongo pygmaeus*), and baboons (*Papio* sp.) suggest that recent humans are more likely to exhibit AMTL than non-human catarrhines (Gilmore, 2013). Humans are more likely to experience AMTL than non-human primates, in part because of significantly longer life histories and the possible association of AMTL with absolute age, but humans remain distinctive even after accounting for these factors (Gilmore, 2013). Behavioral differences between humans and non-human primates may explain the increase in AMTL in humans beyond what is expected from life history/longevity.

It is uncertain where Neandertal AMTL fits in this comparative primate context. At least one study suggested that Neandertals (including Middle Pleistocene hominins believed to be

members of groups ancestral to later, “Classic” Neandertals) have a slightly higher frequency of severe AMTL (in all tooth types combined) than non-human hominoids (Lebel and Trinkaus, 2002), although this study was challenged for not adequately characterizing non-human primate patterns of AMTL (DeGusta, 2002, 2003). Crucially, no studies have compared Neandertals to modern humans. Here, we build on earlier comparisons of AMTL in extant primate taxa, including recent humans (Gilmore and Grote, 2012; Gilmore, 2013), to characterize Neandertal AMTL (all tooth types) relative to humans, chimpanzees, orangutans, and baboons. We further consider the effects of varying the pace of Neandertal life history and of variation among human groups in AMTL.

Materials

Comparative sample

The human comparative sample (Table 1) comes from hunter-gatherer populations from a range of latitudes and northern Eurasian pastoralist populations with limited access to agricultural foodstuffs (Murdock, 1967). The sample is designed to reflect diversity in diet and population history with a particular focus on northern populations living in cold environments with animal-heavy diets similar to those inferred for Neandertals (Richards et al., 2000; Richards and Trinkaus, 2009), without introducing novel behavioral and dietary variables that occur with agriculture. The Afalou, Alaskan, and Californian samples are archaeological. Afalou is a Late Pleistocene cave site in Algeria, dating to roughly 13,000 years ago (Hachi, 1996). The Alaskan sample comes from the Point Hope site in Alaska and dates from about 2,360 to 1,619 BP (Rainey and Ralph, 1959). The Californian remains are from a collection of sites in Central California ranging from about 5,000 to 500 BP (Milliken et al., 2007). Each human population

includes individuals from a broadly similar geographic area and time period (see Supplementary Online Material [SOM] Table 1 for provenience details of each specimen when available), but it undoubtedly encompasses some temporal and spatial variation.

The non-human primate sample includes wild-collected chimpanzees ($n = 61$), orangutans ($n = 38$), and baboons ($n = 75$). The chimpanzee sample derives from various locales in West Africa (SOM Table 2). The orangutan sample comes exclusively from the island of Borneo. The baboon sample includes individuals from across the range of the genus *Papio* and from distinct taxa including yellow ($n = 1$), red ($n = 1$), Chacma ($n = 1$), hamadryas ($n = 34$), and olive ($n = 38$) baboons. Researchers debate the classification of these baboon taxa as species or subspecies, because they are known to hybridize in overlapping zones (Nagel, 1973; Phillips-Conroy and Jolly, 1986) despite substantial social diversity (Altmann, 1974; Dunbar, 1988). Baboons are often characterized as dietary generalists; their diets vary widely depending on local habitat and season, and there appears to be as much intra-taxon variation as inter-taxon variation in diet (Dunbar, 1988; Whiten et al., 1991); so from a dietary perspective, it is reasonable to combine individuals from different taxa into a single baboon sample.

The comparative collections were primarily (sometimes exclusively) composed of individuals of unknown age. We considered an individual to be an adult if at least one third molar was in occlusion; if it seemed likely that the third molars were congenitally absent and attainment of adulthood was questionable, we used complete fusion of the spheno-occipital synchondrosis from the ectocranial surface to distinguish adults. Individuals who did not meet the “adult” criteria were excluded from the sample.

Fossil sample

We selected fossils for inclusion in the sample as objectively as possible to avoid biasing the sample by purposefully including individuals with known dental pathologies. We judged the value of visiting fossil repositories based on the number of fossil specimens curated, proximity to other repositories, and permission granted to access fossils, and then included as many specimens as were made available for study. The sample (Table 2) includes 25 fossil individuals from the sites of Amud, Gibraltar (Forbes' Quarry), Guattari, Krapina, Kulna, La Chapelle-aux-Saints, La Ferrassie, La Quina, Saint-Césaire, Tabun, and Vindija that are generally considered to belong to Neandertals (*Homo neanderthalensis*) on the basis of morphology, provenience, or both. Following Wolpoff (1979), we treat Krapina specimens 50 and 58 as maxillary and mandibular fragments from the same individual.

Unlike for the comparative samples, we included fossil specimens in the sample as long as there was *no* evidence to suggest that the third molar had *not* erupted. Specimens that clearly did not have fully erupted adult dentition were excluded. The specimens that are only tenuously included in the sample as adults include Vindija 225 and Vindija 306. Vindija 225 is a maxillary fragment including sockets from the right second molar to the right central incisor, and Vindija 306 is a portion of the right mandibular body and symphysis, including sockets from the left lateral incisor to the right first molar. Neither specimen has teeth or alveolar bone from third molar sockets to confirm adult status. In the analyses below, both of these specimens are given a very wide age distribution, reflecting lack of knowledge about age (details below).

Methods

Antemortem tooth loss

Exfoliation, the loss of a tooth before death, occurs when the structural support the tooth receives from surrounding periodontal structures (alveolar bone, periodontal ligament, cementum) is sufficiently compromised. Although traumatic injury can result in the immediate loss of teeth, exfoliation of adult teeth is commonly the end result of a gradual process of periodontal remodeling driven by normal senescence (Levers and Darling, 1983; Whittaker et al., 1985; Whittaker et al., 1990), excessive loading, trauma, and/or pathological infection resulting from caries, wear, periodontal disease, or tooth fracture (Clarke, 1986, 1990; Clarke and Hirsche, 1991; Hildebolt and Molnar, 1991). After the tooth is lost, the bone deposition/resorption processes continue until the socket is completely remodeled. At this stage, the socket has been completely filled with trabecular bone and the occlusal surface covered by cortical bone. Typically, the outline of the defunct socket is obliterated and the bone is smooth and depressed relative to the height of the alveolar crests of healthy sockets.

Although the actual exfoliation of the tooth is a binary event, the identification of tooth loss in skeletal remains is necessarily based on the continuous process of alveolar remodeling. Therefore, for every socket without a tooth, the extent of alveolar remodeling was recorded with an ordinal score (1–4, Table 3). A score of 1 indicates a socket that has been completely remodeled and a score of 4 indicates no remodeling (postmortem loss)¹. These ordinal scores can then be sectioned to form three different binary variables that reflect increasing confidence in the antemortem loss of the tooth and a rough estimate of the time since loss. The most liberal combination (i.e., results in the highest frequencies of AMTL) of alveolar remodeling scores considers AMTL to be present for scores 1–3 and absent for score 4. A more moderate combination considers AMTL to be present for scores 1–2 and absent for scores 3–4. The most

¹ Occasionally, a tooth may be injured or worn to a point where only the root below the occlusal level of the alveolar bone remains. Alveolar resorption often does not occur in these cases although the root is functionally absent. When we encountered this situation, we recorded the tooth as present but severely broken.

conservative combination considers AMTL to be present only for score 1 when the socket is completely resorbed. Many researchers, following Buikstra and Ubelaker (1994), appear to follow methods most similar to the liberal combination scheme, although few studies explicitly discuss what is considered acceptable evidence of remodeling for the identification of AMTL.

For each individual, the first author recorded the number of sockets observable for AMTL (that is, present and unobstructed), the presence/absence of a tooth, and, if the tooth was not present, the alveolar resorption score (1–4). Every observable tooth in an individual's dental arcade was considered regardless of tooth type. Table 2 presents the data for each of the fossil specimens, and Table 4 presents summaries for each non-human primate taxon and each human population. The first author further recorded molar wear following Scott (1979) for each quadrant of every molar on the left side, except in cases of obvious asymmetry in which case both sides were scored, or lack of preservation on the left side in which case the right side was scored. We averaged the scores for each quadrant (Li and Ji, 1995) and for the mandibular and maxillary first, second, and third molars. We then used the difference between the first and second molar wear scores to calculate average wear rates in units of Scott's score per year for each taxon (Gilmore and Grote, 2012). Unlike the AMTL recording, only molars were used to calculate wear rates.

Binomial regression modeling

An investigation of AMTL is inherently hierarchical. There are sockets within individuals, individuals within populations, and populations within taxa. Measures at each level can be informative. For example, the total number of sockets with AMTL relative to the total

number of sockets observed gives us an estimate of the AMTL experience of a given individual or group of individuals. Explanations linking AMTL survival to behavior focus on the individual level, specifically, the frequency of individuals with a high proportion of their dentition lost antemortem. Prior exploration of the comparative dataset suggests that there are several other important variables to consider when comparing AMTL among groups. An individual's age-at-death is particularly informative (Gilmore, 2013). Age-at-death represents the period of risk for many pathological conditions and as such is an important variable in paleopathological analysis (Waldron, 1991). Furthermore, age is expected to progressively increase the risk of exfoliation via age-dependent changes in the dentition such as dental wear and continuous eruption. Like age, tooth type (anterior, premolar, or posterior) also appears to contribute to the chance of tooth loss. Teeth from the posterior (molar) regions are more likely to be lost than either premolar or anterior teeth (Gilmore, 2013).

One way to investigate the factors associated with AMTL is to treat the number of sockets lost antemortem as binomial counts, which makes various multi-level binomial regression models available. These models take advantage of the hierarchical nature of the data while quantifying variation due to age and tooth class. Taking a Bayesian approach using the Gibbs sampler (implemented in Winbugs; see Lunn et al., 2000) further allows for the inclusion of covariate measurement error (e.g., error in the estimation of age-at-death) by iteratively sampling from the conditional distribution of each unknown parameter given values for the remaining parameters. Given sufficiently uninformative priors, this method will produce inferences similar to those of maximum likelihood methods.

Missing data in the Neandertal dataset are handled seamlessly in the binomial regression model, because the observations are treated as binomial counts at the socket level rather than as

proportions of AMTL at the individual level. The models treat each of an individual's preserved sockets as a "test." Individuals with more "tests" are more informative for estimating the parameters of the model. The incompleteness of the fossil sample affects confidence in the estimate of the average tooth loss experience for the group from which the fossil sample derives (i.e., standard deviation of the estimate), but it does not change the way this sample is dealt with when the model is fit.

Each binomial model compared here predicts the number of sockets with AMTL ($Y_{t[i],s[i]}$) in any given tooth class t of individual i in taxon s based on the number of sockets observable ($N_{t[i],s[i]}$) and the probability ($p_{t[i],s[i]}$) that any given tooth will be lost antemortem. The probability that the tooth is lost antemortem is estimated from the data based on the tooth class in question (anterior, premolar, or posterior), taxon, and age (AGE_i) of the individual. Each model is defined mathematically in the Appendix. Tooth class and taxon are categorical variables that are interpreted as a change in the probability of AMTL relative to a baseline; here, the baseline is the probability of observing AMTL in human anterior sockets. In contrast, age (AGE_i) is a continuous variable measured with error. For each individual, at each iteration of the Gibbs sampler, a candidate age is randomly generated from a normal distribution defined with mean AGE_i and standard deviation $\hat{\sigma}_i^2$. AGE_i is an estimate of the age-at-death of each individual and $\hat{\sigma}_i^2$ is an estimate of the error in the associated age-at-death estimate, discussed in detail below. The models also allow for heterogeneity in individual susceptibility via inclusion of an individual-level random effect Z_i . The model estimates the random effect at each iteration by assuming a normal distribution of susceptibility with mean zero and a standard deviation (σ_Z) estimated by pooling information about variation across the dataset. Prior exploration of the dataset suggests that sex is not a strong predictor of AMTL and that the data are insufficient to

identify taxon-specific interactions of age or tooth type with AMTL (Gilmore, 2013), so neither sex nor interaction effects are included in any of the models discussed here. The “Main Effects” models contain each of the parameters discussed above.

Humans are a particularly variable species, living at vastly different latitudes and having correspondingly diverse diets. In the interest of exploring variation among human populations and its effect on the interpretation of between-taxon differences, we compare the Main Effects models to a second class of model, the “Population Effect” models, which allow for inter-population heterogeneity among human populations with a random effect ϕ_i , in addition to the rest of the Main Effects parameters. This population-level random effect is calculated in the same manner as the individual-level random effect ($N(0, \sigma_i^2)$), except that it pools information about variation across the human populations rather than across individuals.

All calculations were executed in R 2.11.1 and WinBUGS1.4 (see SOM Appendix 1). Diffuse priors for all parameters were defined as a normal distribution with a mean of 0.0 and a standard deviation of 50. The random effects (both individual-level and population-level) were assumed to be normal with mean zero and variance sigma squared; the prior distribution for each sigma was uniform on the interval 0 to 50. Gibbs sampler procedures for every model were the same: a single chain of 505,000 iterations, discarding the initial 5,000 as a “burn-in” and retaining every 50th sample for analysis. These procedures resulted in a total of 10,000 samples for each parameter.

Age-at-death

Comparative sample. Many specimens in the dataset are represented only by cranial remains, making estimation of the age-at-death challenging. For every individual in the comparative sample with at least one molar remaining, we used a modification (Gilmore and Grote, 2012) of the Miles method (Miles, 1962, 1963) based on extrapolating wear rates from adult wear gradients to estimate age ($\hat{AGE}_i$) and error in the age estimate ($\hat{\sigma}_i^2$) in years. The estimates are preferentially based on the first molar, relying on the second molar only when at least one first molar was not available or had reached a maximum wear stage, and the third molar only when neither the first nor the second molars were available. The age estimate and associated error (in the form of a standard deviation) define a normal distribution of age for each individual from which the models sample iteratively.

If all molars were missing, either ante- or post-mortem, we used cranial sutures to estimate age and error following Meindl and Lovejoy (1985). We excluded individuals for which neither molars nor cranial sutures were preserved and AMTL was less than 25% of the preserved dentition. Individuals missing many teeth antemortem are an important component of the sample; when neither molars nor cranial sutures were preserved for individuals with significant AMTL, we followed suggestions that individuals with significant AMTL are above 50–60 years of age (Mays, 1998; Miles, 2001) and assigned individuals with more than 50% of their preserved teeth lost antemortem to an age category of 50 ± 15 years. Individuals with less than 50% but more than 25% of their teeth lost antemortem were assigned to age 40 ± 10 . This procedure introduces an element of circularity to the relationship of age and AMTL, and was used only when absolutely necessary. Only 13 specimens were aged using this method. In the comparative sample, only human specimens required the use of methods other than the modified Miles method to estimate age.

The fossil sample. The modified Miles method requires knowledge of the age of eruption of the first and second molars, their correlation, and intra-population variation in eruption ages to estimate age and the error in each age estimate (Gilmore and Grote, 2012). These data are available for humans and many of the non-human primate taxa included here (Gilmore, 2013), but are largely unknown for fossil hominin taxa. To reflect this uncertainty, we assign two different age-at-death estimates for each Neandertal specimen: the first (*Modern Age*) is based on human-like growth and senescence and the second (*Rapid Age*) is reduced to reflect the possibility of a more rapid life history (see details below). Like the comparative sample, each age estimate is in the form of an average age and associated standard deviation that are passed to the models to define a normal distribution. The Main Effects model and Population Effect models are each run twice, once with *Modern Age* and once with *Rapid Age* estimates for the fossils to compare the effect of different age estimates on the model predictions. The comparative sample ages are the same regardless of the estimates used for fossils.

The *Modern Age* estimate applies modern human aging standards to skeletal (usually dental) indicators to estimate age for each fossil. When at least one adult molar was preserved, we used the modified Miles method as described above to estimate age-at-death and associated error for fossil specimens assuming modern human estimates of molar eruption, correlation, and variation. Trinkaus (1995, 2011) presents categorical age estimates (20–40 and > 40 years) for a large sample of Late Pleistocene fossils that summarize personal observations and published literature applying human aging standards to any available age-indicator. In all but one case, our age estimates from the modified Miles method fall within Trinkaus' age category (Fig. 1), often quite close to the midpoint of the young adult category and the lower end of the unbounded older

adult category. The only exception is Kulna 1, which Trinkaus (1995) places in an adolescent age category between 10 and < 20 years old. Our wear-based method returns a slightly older estimate of 23 years.

Guattari 1, Gibraltar 1, Krapina 49, Krapina 56, Vindija 225, Vindija 250, and Vindija 306 lack molars from which to make wear-based estimates. For the first two specimens, we assigned a midpoint of 45 years to Trinkaus' (1995, 2011) older adult category and use this as the age estimate for both individuals. We use the linear equation that describes the relationship between estimated age and error in our Neandertal sample (approximately $\hat{\sigma}_1^2 = -1.27 + 0.23 * AGE_1$) to calculate a standard deviation of 9.31 years for an estimated age of 45 years. For both Krapina specimens, we used Wolpoff's (1979) wear-based estimates from non-molar teeth; the age estimates for Krapina 49 and 56 are based on their similarity in wear to Krapina 48, which Wolpoff (1979) estimated to be approximately 16 years old after accounting for his observation that Neandertals likely erupted their third molars slightly earlier than modern humans. If modern human schedules had been strictly applied, all of these individuals would have had age estimates two to three years older. However, our age estimate from the first molar of Krapina 48 is quite close to Wolpoff's (1979) estimate, despite assuming a human-like eruption of the first molar. For this reason, we use Wolpoff's (1979) estimates for Krapina 49 and 56 without adjustment. As with Guattari 1 and Gibraltar 1, we use the relationship between age and error from our own data to estimate standard deviations for Wolpoff's (1979) age estimates of Krapina 49 and 56. Vindija 225, 250, and 306 lack precise age estimates entirely. Vindija 250 preserves a third molar socket, so it is confidently an adult; the other two fragments do not preserve evidence of the third molar or evidence of juvenile status. In the absence of precise estimates, we assigned Vindija 250 an age of 35 with a standard deviation of 10 and the

other two specimens an age of 30 with a standard deviation of 15. These estimates correspond to age distributions for each individual that span the majority of the lifespan within one to two standard deviations.

Some recent histological studies of Neandertal juvenile dentition suggest that Neandertals developed and erupted their dentition more rapidly than modern humans (Ramírez-Rozzi and Bermúdez de Castro, 2004; Smith et al., 2007; Smith et al., 2010). Smith and colleagues (2010: Supplementary Table 7) compare histologically based age estimates to estimates from modern human calcification standards in the most comprehensive review available; on average, the histological age estimates are only 82% of the estimates from modern human standards. Assuming this relationship is constant through life, we multiply *Modern Age* by 0.82 and create the second, reduced age estimate called *Rapid Age*. The standard deviations are calculated using the same regression equation as above.

Results

Table 4 presents the number of sockets observed, the percentage of those sockets with AMTL for each taxon, and each binary method of scoring AMTL. For each individual, we calculated the proportion of sockets lost antemortem relative to sockets observed. The individual proportions then form a distribution (Fig. 2) for each taxon; summary statistics are presented in Table 5. Table 6 presents these distributions in a tabular form comparable to Lebel and Trinkaus (2002). As expected, different scoring methods result in very different absolute estimates but do not substantially change the patterning across taxa. As a whole, humans have a higher frequency of AMTL than any other taxon, including Neandertals. Neandertals appear to be intermediate

between humans and chimpanzees, although they are more similar to chimpanzees than to humans, and have much higher frequencies of AMTL than observed in either orangutans or baboons. Importantly, the measurements in these tables do not account for potential differences in the composition of the samples; for example, the ages of the individuals represented or the proportional representation of tooth types.

The binomial models allow variation in AMTL to be partitioned among these variables, separating variation due to age, tooth type, and taxon. The results from each model are reported in Table 7. The addition of Neandertals to the sample does not significantly change relationships between AMTL and age or tooth type that were observed previously in the comparative sample (Gilmore, 2013). Relative to the anterior teeth, odds of AMTL are higher in posterior teeth and lower in premolar teeth. On average, each additional decade of age roughly triples the odds of AMTL. The standard deviation of the individual-level random effect (σ_{ϵ}) is also proportionally large, indicating that there is considerable variation between individuals that is not explained by any of the predictor variables in the model (Gilmore, 2013).

Main Effects models

Once variation in age and tooth type is taken into account, the odds of AMTL in chimpanzees, baboons, and orangutans from the Main Effects models are on average 0.20, 0.11, and 0.05 times the odds of AMTL in humans, respectively (Gilmore, 2013). When Neandertals are added to the analysis, these values only change slightly (0.23, 0.11, 0.05). The positioning of Neandertals relative to the other taxa in Main Effects models depends on which ages are used. Using modern human aging schedules, the odds of AMTL for Neandertals are on average only

0.17 times the human odds, which is *lower* than chimpanzees though still higher than either baboons or orangutans. This suggests that for a given age and tooth type, Neandertals are less likely to have AMTL than either humans or chimpanzees. The smaller sample size of Neandertals makes a rare event, such as AMTL, less likely to be observed. This uncertainty is reflected by the standard deviations associated with the average effect size estimates in Table 7. A 95% posterior credibility density of the Neandertal contrast still does not overlap with the modern human average (denoted by the vertical line marking 0.0 in Fig. 3), though Neandertal and chimpanzee distributions overlap substantially. In contrast, when a rapid life history is assumed for Neandertals and the ages are reduced, the odds of AMTL in Neandertals more than double, increasing to 0.37 times those of humans and surpassing those of chimpanzees. The result is driven by the strong positive relationship between age and AMTL (Fig. 4). The average Neandertal estimate is still markedly lower than for modern humans and similar to chimpanzees, but it overlaps the average human intercept two standard deviations from the average effect estimate.

Population Effect models

The Population Effect models differ from the Main Effects models only in that they include a population-level random effect for the human populations. This random effect accounts for substructure and inter-population variation in the human sample by pooling information from each population to adjust the human average. The Population Effect models suggest a population-level random effect standard deviation as large as that of the individual random-effect—signaling substantial variation between populations. Figure 5 plots the 95% posterior

credibility densities for each human population and non-human primate taxon as compared to the overall human average. The Afalou sample stands out as having the highest average odds of AMTL observed—a relative placement that conforms to prior expectations regarding this sample given the attribution of the Afalou remains to the Iberomaurusian. The Iberomaurusian culture is often characterized by intentional dental ablation of the upper central incisors (Lubell et al., 1984), a practice that is strongly suspected to be responsible for AMTL in eight of the individuals included in this sample (Gilmore, pers. obs.). If AMTL in the anterior tooth class is discarded, the Afalou sample becomes more similar to the human average (results not shown). The human populations with the lowest odds of AMTL—Fuegian, Chukchi, and Sami—are among those with hunting-focused subsistence that likely incorporates a lower proportion of fibrous plant foods into the diet and is associated with lower estimated wear rates. However, the high-latitude Buriat and Alaskan populations, with diets expected to be similar to the Chukchi and Sami, have larger odds of AMTL.

One difference between the Fuegian, Chukchi, and Sami populations and the Buriat and Alaskan populations is that the samples of the former are smaller than those of the latter. Accordingly, one possible explanation for this contrast is that the posterior probability distributions for small samples are biased, so that small samples always appear to have low odds of AMTL. However, a further analysis suggests that this is not the case. In Figure 5, the Chukchi and Sami have very similar posterior means, and the distributions are shaped similarly, so we combined these two samples into a single group and ran the model again. The combined group has a similar sample size (number of sockets) as the Buriat and Afalou samples, but its posterior mean is almost identical to the posterior means of the separate Chukchi and Sami samples (results not shown), and much lower than the Buriat and Afalou posterior means. This additional

analysis suggests that the posterior distributions for small samples, including the Neandertal sample, reliably reflect the odds of AMTL.

Considering between-population variation within the human species reduces the difference in AMTL odds between humans and all non-human primate taxa and increases the uncertainty estimates associated with each taxon contrast. Though the non-human average odds are still smaller than the human average, the 95% credibility densities suggest ample overlap between humans and all non-human primates (Fig. 5). In fact, variation among human populations encompasses the variation between humans and non-human primates.

The difference between the Population Effect models using *Modern Age* and *Rapid Age* estimates for the fossils mimics that observed between the two Main Effects models: Neandertal average odds of AMTL relative to the human average increases when ages are decreased, moving from a position below chimpanzees with *Modern Age* to a position closer to modern humans with *Rapid Age*. Even with *Modern Age* estimates, the Neandertal average is quite similar to that of the Sami and Chukchi—northern Eurasian pastoralists with some of the lowest odds of AMTL among the human populations—and with *Rapid Age* estimates the Neandertal average moves closer to the human average.

Discussion

Lebel and Trinkaus (2002) argue that Middle and Late Pleistocene fossil hominins have a higher frequency of individuals with severe AMTL than do extant hominoids. DeGusta (2002, 2003) disagrees, suggesting instead that the results are more consistent with a null hypothesis of no difference. The analyses presented here could be used to support either interpretation

depending on the assumptions. If Neandertals are assumed to senesce at a rate per year similar to modern humans, then they have average odds of exhibiting AMTL much lower than modern humans and somewhat lower than chimpanzees. The substantial overlap between the 95% credibility densities of the chimpanzee and Neandertal estimates suggest these taxa are similar and support DeGusta's (2002, 2003) interpretation that Neandertals and chimpanzees are similar in AMTL. A more human-like estimate for Neandertals, *sensu* Lebel and Trinkaus (2002), could be observed if Neandertals are assumed to have a more rapid life-history than modern humans. In this case, the younger age estimates for the Neandertals increase their average odds of AMTL at a given age to a level intermediate between humans and chimpanzees. The estimate is still slightly closer to the chimpanzee average, but the credibility density does overlap the average human estimate.

That recent humans have higher odds of AMTL on average than any non-human primate does provide some support for an association between AMTL and uniquely modern human characteristics; however, confidence in this association is weakened when variation among human populations is considered. There is substantial variation among human populations—as great as that between humans and non-human primates (Fig. 5)—that suggests that human AMTL can vary considerably due to variables not included in the binomial analyses. Several human populations have odds of AMTL similar to non-human primates. When this substructure is considered, it reduces the overall human average and increases the uncertainty in the estimation of between-taxon contrasts. The fact that all recent human populations do not universally exhibit high odds of AMTL, despite sharing modern behavior and life history, complicates behavioral interpretations of AMTL, but it may still be the case that modern human behaviors reduce AMTL-related mortality.

Consider the etiology of AMTL and the creation of skeletal assemblages from living populations. As discussed above, AMTL most often results from a continuous process, alveolar remodeling, that can result from normal senescence and a number of pathological conditions. Two of the most important contributors, attrition and caries, are heavily influenced by diet, oral chemistry, and paramasticatory tooth use, which are all factors that vary widely across human (and non-human) populations (Larsen, 2002; e.g., Molnar, 1971, 1972). Paramasticatory use of the dentition may also explain distinctive wear patterns in anterior dentition of Neandertals (Brace, 1962; Smith and Paquette, 1989). Variation in pathological conditions that lead to AMTL thus results in variation in the *risk* of having AMTL among human populations (and indeed, among individuals within populations). Variation in *frailty*, or likelihood of death as a result of AMTL, may also vary among populations, which contributes to variation in the creation of skeletal assemblages from living populations (Wood et al., 1992; Goodman, 1993; Cohen et al., 1994).

For two living populations with equal frailty (equal chance of death), the population with the higher risk for AMTL is expected to have more AMTL than the population with the lower risk for AMTL. However, when frailty is high (death is likely), the average AMTL frequency of a population cannot rise above the level at which death typically occurs. As frailty is reduced, this constraint is relaxed and potential variation in AMTL frequencies is increased. In this case, differential risk of AMTL would result in widely varying AMTL frequencies among individuals and populations—a situation that seems to fit with the substantial variation observed among human populations. This theoretical relationship suggests that the low average odds of AMTL in fossil hominins is not diagnostic of mortality. It is compatible either with low frailty and low risk, or high frailty (and either low or high risk). In contrast, high levels of AMTL can only result

from low frailty. If Neandertal molars erupted at similar ages as modern humans, then Neandertals would have molar wear rates at the lower end of human variation (see Table 4 in this paper and Table 3 in Gilmore and Grote [2012] for wear rates by population); Neandertals also have low rates of caries (Brothwell, 1963; Brennan, 1991; Trinkaus et al., 2000), which taken together, may suggest that Neandertals had a low risk of AMTL relative to an average human of a similar age rather than high mortality from AMTL.

Conclusions

The results presented here show that recent humans have higher odds of AMTL on average than chimpanzees, orangutans, baboons, and Neandertals. Neandertals have levels of AMTL most similar to those of chimpanzees, although the estimates depend, in part, upon the estimated ages of the Neandertal individuals. Neandertals could have higher levels of AMTL than non-human primates if they are assumed to have faster life histories than modern humans, but even so, the average Neandertal estimates fall at the lower end of human variation. However, the substantial inter-population variation observed among recent human populations suggests that if AMTL-related mortality is behaviorally mediated, as has been proposed, only high frequencies of AMTL would be diagnostic of behavior. Consequently, the behavioral implications of low frequencies, such as those found for Neandertals, are ambiguous. Estimates of Neandertal AMTL experience are not different enough from non-human primates that they require behavioral explanations, but neither do these results exclude modern human behaviors from the Neandertal repertoire.

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Appendix

Main Effects Model:

$$y_{t[i],s[i]} \sim \text{Binomial}(n_{t[i],s[i]}, p_{t[i],s[i]})$$

$$p_{t[i],s[i]} = \text{logit}^{-1}(\mu_{t[i]} + \beta_{s[i]} + \delta * AGE_i + \mathbb{Z}_i)$$

$$\mu_{t[i]} = a_0 + b_0 * [t=post] + c_0 * [t=pri]$$

$$\beta_{s[i]} = \alpha_1 * [s=post] + b_1 * [s=pri] + c_1 * [s=neand] + d_1 * [s=pan] , \text{ where}$$

$$AGE_i \sim N(AGE_i, \sigma_1^2), \mathbb{Z}_i \sim N(0, \sigma_2^2), [t=post], [t=pri], [s=neand], [s=pri], [s=pan], \text{ and } [s=neand]$$

are binaries indicating group membership in tooth class posterior, tooth class premolar, taxon

Homo neanderthalensis, taxon *Pan*, taxon *Papio*, and taxon *Pongo*, respectively, and $y_{t[i],s[i]}$,

$n_{t[i],s[i]}$, AGE_i , σ_1^2 , and σ_2^2 are as defined in text above. Note that AGE_i and σ_1^2 change for the

fossil specimens depending on whether *Modern Age* or *Rapid Age* is used.

Population Effects Model

$$y_{t[i],s[i],p[i]} \sim \text{Binomial}(n_{t[i],s[i],p[i]}, p_{t[i],s[i],p[i]})$$

$$p_{t[i],s[i],p[i]} = \text{logit}^{-1}(\mu_{t[i]} + \beta_{s[i]} + \delta * AGE_i + \mathbb{Z}_i + \theta_{p[i]})$$

$$\mu_{t[i]} = a_0 + b_0 * [t=post] + c_0 * [t=pri]$$

$$\beta_{s[i]} = \alpha_1 * [s=post] + b_1 * [s=pri] + c_1 * [s=neand] + d_1 * [s=pan]$$

$$\theta_{p[i]} = \Psi_{p[i]} * [p=H.sapiens] , \text{ where}$$

$$\Psi_{p[i]} \sim N(0, \sigma_p^2) \text{ and all other variables are as defined in the Main Effects model above. } p[i]$$

indicates membership in a *Homo sapiens* population for individual i .

Figure legends

Figure 1. Neandertal ages estimated with the modified Miles method as compared to Trinkaus' (1995, 2011) estimated age categories. La Chapelle-aux-Saints and La Ferrassie II are each placed in an age category from 30–50 years, following Trinkaus' (1995) contention that these individuals are likely at the upper end of the young adult category or the very low end of the older adult category. With the exception of Kulna 1, there is a close correspondence between the estimated ages.

Figure 2. Kernel density plots of proportional AMTL observed in each taxon. The x-axis represents the proportion of teeth lost relative to sockets observed in an individual. The y-axis summarizes the distribution of individuals with a smooth curve that integrates to one—the density represents the fraction of individuals in the sample having AMTL proportions in a small neighborhood $(x - \frac{dx}{2}, x + \frac{dx}{2})$ around the value x , given approximately by $y(x) * dx$. Orangutan and baboon densities are not shown in this figure; their proportions of AMTL are so small that figures on the scale shown here are uninformative.

Figure 3. Posterior Density plots of the taxon parameters in the Main Effects model. Each plot shows the density of 10,000 samples from the Bayesian posterior distribution for the taxon parameters of the Main Effects model, which are given relative to the human mean. Black distributions show 95% posterior credibility densities for the Main Effects model using *Modern Age* for Neandertals. The dotted line shows the Neandertal density for Main Effects model with *Rapid Age*. The effects for other taxa are changed imperceptibly when *Rapid Age* is used for the fossil sample and are not shown here.

Figure 4. Main Effects model predictions by age. This figure plots the average predicted log odds of AMTL from the Main Effects model for each taxon against age. Taxa are constrained to share the same relationship (slope) with age, but the intercept is allowed to vary.

Figure 5. Posterior Density plots of the parameters in the Population Effects model. Each plot shows the density of 10,000 samples from the Bayesian posterior distribution for the parameters of the Population Effects model. Gray curves are 95% posterior credibility densities of each human population used in the estimation of the population-level random effects. Black curves show the effect sizes and 95% posterior credibility densities for the Population Effects model using *Modern Age* for Neandertals. The dotted lines show the Neandertal distribution for the Population Effects model using *Rapid Age*. The effects for other taxa are changed imperceptibly when *Rapid Age* is used for the fossil sample and are not shown here.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

TABLES

Table 1. Composition of the human comparative sample.^a

Population	Region	Subsistence	N
Afalou*	Algeria, Africa	Hunting/gathering	23
Alaska*	Point Hope, Alaska	Fishing/hunting	41
Australian	Australia	Gathering and hunting	69
Buriat	Siberia	Animal husbandry and hunting	27
Chukchi	Siberia	Animal husbandry and hunting/fishing	16
Fuegian	Patagonia	Fishing/hunting	9
Khoi-San	South Africa	Gathering and hunting	38
Native American*	Central California	Gathering and hunting	74
Sami	Norway	Animal husbandry and fishing	13

Total: 310

^a Sample size and a generalization of the subsistence mode are provided. The “Subsistence” column lists the top two components (in order of relative importance) of the subsistence economy of each group based on ethnographic observations of modern hunter-gatherers in the same region (Murdock, 1967).

*Archaeological samples that in each case have been assigned to Murdock’s (1967) subsistence categories. Archaeological evidence associated with the Epipaleolithic hunter-gatherers of Afalou suggests a hunting-driven economy with some use of shellfish; little evidence for plant use is available archaeologically but it is assumed given the paleoenvironment of the area (Lubell, 2001).

A slash is used to denote uncertainty in the order of relative importance. We classify the subsistence of the Ipiutak of Point Hope, Alaska as “Fishing/hunting” on the basis of archaeological evidence and dental microwear patterns that suggest the Ipiutak had a meat-heavy diet that included both inland and marine resources (Larsen and Rainey, 1948; El-Zaatari, 2008). The Native Californian samples are classified as “Gathering and hunting” on the basis of zooarchaeological and paleobotanical results suggesting a reliance on mammals, fish, and acorns with increasing intensification through time (Broughton, 1994; Wohlgemuth, 1996).

Table 2. Neandertal sample.^a

Specimen	# Sockets	AMTL (conservative)	AMTL (moderate)	AMTL (liberal)	Modern Age ($\overline{AGE}_1$)	St. Dev (σ_1^2, σ_1^2)
Amud 1	24	0	0	0	33.59	6.62
Gibraltar 1	16	0	1	3	45.00	9.31
Guattari 1	10	6	8	10	45.00	9.31
Guattari 2	12	1	1	3	41.42	6.09
Guattari 3	15	0	0	0	30.81	5.96
Krapina 48	5	0	0	0	14.69	2.23
Krapina 49	6	0	0	0	16.00	2.49
Krapina 50/58	21	0	0	0	30.81	5.96
Krapina 56	9	0	0	0	17.00	2.73
Krapina 57	13	0	0	0	29.57	5.67
Krapina 59	16	1	1	1	30.19	5.82
Kulna 1	7	0	0	0	23.37	4.22
La Chapelle-aux-Saints 1	28	7	9	14	42.66	6.38
La Ferrassie II	6	0	0	0	45.68	9.48
La Quina 5	10	0	0	0	33.90	6.70
La Quina 9	9	0	0	0	30.81	5.96
Saint-Césaire 1	19	0	0	0	30.19	5.82
Tabun C1	31	0	0	0	31.42	6.11
Vindija 206	10	0	0	0	30.81	5.96
Vindija 225	7	0	0	0	30.00	15.00
Vindija 226	11	0	0	0	30.81	5.96
Vindija 231	11	0	0	0	34.52	6.84
Vindija 250	4	0	0	0	35.00	10.00
Vindija 259	8	0	0	0	32.74	4.13
Vindija 306	8	0	0	0	30.00	15.00

^a The columns give the number of sockets considered observable for antemortem tooth loss (AMTL), the number of sockets with AMTL based on each method of combining alveolar resorption scores into a binomial variable, the age in years estimated with the application of modern human standards (*Modern Age*), and the estimated error in age estimation in the form of a standard deviation in years. All tooth types are included in the socket and AMTL counts.

Table 3. System of scoring alveolar resorption.^a

Score	Description of the Appearance of the Alveolar Bone			
	<i>Socket</i>	<i>Regularity</i>	<i>Porous Bone</i>	<i>Interpretation</i>
0	N/A	N/A	N/A	Not observable
1	Completely obliterated	N/A	Large or not porous	Definite AMTL
2	Less than 2 mm	Irregular	Large	Some resorption
3	More than 2 mm	Irregular	Some large, most regular	Beginning resorption
4	Completely formed	Clearly defined	Small porous bone	Postmortem tooth loss

^a Each score is determined based on the depth of the remaining socket and the appearance of the alveolar bone. Regularity refers to the shape of the socket walls and porosity to the size of the pores in the alveolar bone of the socket.

Table 4. Percentage of sockets with dental pathology.^a

Taxon	N	AMTL %	AMTL % (moderate)	AMTL % (liberal)	Molar Wear Rate
Humans	8247	7.89	10.15	14.70	0.28
Neandertals	331	4.53	6.04	9.37	0.20
Chimpanzees	1917	1.98	2.14	3.60	0.24
Baboons	2264	0.39	0.39	0.62	0.40
Orangutans	1105	0.18	0.18	0.45	0.51

^a N (AMTL) reports the number of sockets observable for AMTL in each sample. The other columns provide the AMTL percentage of the total number of sockets observed for each method of combining alveolar resorption scores. Also reported are average molar wear rates in units of Scott's score (1979) per year for each taxon (assuming modern human eruption schedules for the Neandertal sample). All tooth types are included in the AMTL counts and percentages.

Table 5. Proportion of teeth lost antemortem within individuals.^a

Taxon	N	Mean	Std	Max	97.5% quartile
Humans	310	0.081	0.166	1.000	0.705
Neandertals	25	0.040	0.128	0.600	0.390
Chimpanzees	61	0.020	0.065	0.375	0.219
Baboons	75	0.004	0.013	0.062	0.037
Orangutans	38	0.002	0.010	0.062	0.005
Humans	310	0.104	0.192	1.000	0.844
Neandertals	25	0.053	0.169	0.800	0.513
Chimpanzees	61	0.021	0.066	0.375	0.221
Baboons	75	0.004	0.013	0.062	0.037
Orangutans	38	0.002	0.010	0.062	0.005
Humans	310	0.153	0.232	1.000	0.875
Neandertals	25	0.080	0.223	1.000	0.700
Chimpanzees	61	0.038	0.095	.0406	0.365
Baboons	75	0.006	0.017	0.094	0.0625
Orangutans	38	0.005	0.017	0.062	0.0625

^a The proportion of teeth lost antemortem relative to sockets observable for AMTL (all tooth types included) were calculated for each individual. This table presents descriptive statistics summarizing the distribution for each taxon.

Table 6. Number (percent) of individuals with percentage of teeth lost antemortem (all tooth types included) in 10% increments when tooth loss is scored moderately.

% lost AM	Humans	Neandertals	Chimpanzees	Baboons	Orangutans
0–1%	162 (52.26)	20 (80.0)	51 (83.61)	68 (90.67)	37 (97.37)
> 1–10%	61 (19.68)	3 (12.0)	6 (9.84)	7 (9.33)	1 (2.63)
> 10–20%	37 (11.93)	0	2 (3.28)	0 (0)	0 (0)
> 20–30%	14 (4.52)	0	1 (1.64)	0 (0)	0 (0)
> 30–40%	17 (5.48)	1 (4.0)	1 (1.64)	0 (0)	0 (0)
> 40–50%	3 (0.97)	0	0 (0)	0 (0)	0 (0)
> 50–60%	4 (1.29)	0	0 (0)	0 (0)	0 (0)
> 60–70%	0 (0)	0	0 (0)	0 (0)	0 (0)
> 70–80%	3 (0.97)	1 (4.0)	0 (0)	0 (0)	0 (0)
> 80–90%	7 (2.26)	0	0 (0)	0 (0)	0 (0)
> 90–100%	2 (0.64)	0	0 (0)	0 (0)	0 (0)
N	310	25	61	75	38

Table 7. Summary statistics for binomial-normal regression model parameters.

Model	Main Effects (<i>Modern Age</i>)		Main Effects (<i>Rapid Age</i>)		Population Effect		Population Effect (<i>Rapid Age</i>)	
DIC ^a	1780.13		1780.30		1770.76		1771.56	
Parameter	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept (α_0)	-5.390	0.289	-5.393	0.284	-6.073	0.841	-6.159	0.918
Premolar (α_0)	-0.278	0.121	-0.278	0.120	-0.280	0.122	-0.278	0.122
Posterior (α_0)	0.585	0.101	0.585	0.107	0.587	0.100	0.587	0.101
Neandertal (α_1)	-1.755	0.796	-1.001	0.771	-1.198	1.098	-0.221	1.153
<i>Pan</i> (α_1)	-1.477	0.534	-1.496	0.530	-0.726	0.942	-0.652	1.004
<i>Papio</i> (α_1)	-2.222	0.618	-2.224	0.629	-1.301	0.992	-1.231	1.056
<i>Pongo</i> (α_1)	-3.050	1.259	-3.040	1.240	-1.882	1.423	-1.831	1.483
Age (α)	0.115	0.015	0.115	0.015	0.139	0.016	0.139	0.0167
Indiv Random Effect (α_i)	--	2.212	--	2.214	--	2.036	--	2.042
Pop Random Effect ($\alpha_{i,j}$)	--	--	--	--	--	2.023	--	2.050

^aDeviance Information Criterion: a measure of the trade-off between goodness of fit and complexity