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Is Human Longevity a Consequence of Cultural Change or Modern Biology?

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ABSTRACT Increased longevity, expressed as the number of individuals surviving to older adulthood, represents a key way that Upper Paleolithic Europeans differ from earlier European (Neandertal) populations. Here, we address whether longevity increased as a result of cultural/adaptive change in Upper Paleolithic Europe, or whether it was introduced to Europe as a part of modern human biology. We compare the ratio of older to younger adults (OY ratio) in an early modern human sample associated with the Middle Paleolithic from Western Asia with OY ratios of European Upper Paleolithic moderns and penecontemporary Neandertals from the same region. We also compare these Neandertals to European Neandertals. The difference between the OY ratios of modern humans of the Middle and Upper Paleolithic is large and significant, but there is no significant difference between the Neandertals and early modern humans of Western Asia. Longevity for the West Asian Neandertals is significantly more common than for the European Neandertals. We conclude that the increase in adult survivorship associated with the Upper Paleolithic is not a biological attribute of modern humans, but reflects important cultural adaptations promoting the demographic and material representations of modernity. Am J Phys Anthropol 129:512–517, 2006.

Increased longevity, expressed as the proportion of adults surviving to older adulthood, represents an important way that Upper Paleolithic Europeans differ from earlier European populations. In a recent study comparing Neandertals with their Upper Paleolithic anatomically modern successors, we showed a fivefold increase in the ratio of older to younger adults (OY ratio, a categorical assessment) in the Upper Paleolithic (Caspari and Lee, 2004). We suggested that the increase in longevity we documented was associated with the demographic and cultural changes marking that period (Templeton, 2002; Shennan, 2001). However, it was unclear whether this increase in older adult survivorship is an attribute of the Upper Paleolithic itself, or whether it was already present in earlier anatomically modern humans migrating into Europe from elsewhere. In this paper, we address this question, using data that include pivotal fossil material from Western Asia and an expanded sample of European modern humans.[1]

Our question is whether the increase in adult survivorship is a biological attribute of a modern human species, or whether nonphylogenetic causes for longevity may be more explanatory, such as culturally driven demographic change (Shennan, 2001). Here, we address this issue with three sets of comparisons. 1) We compare the OY ratio of earlier modern humans associated with the Middle Paleolithic of Western Asia with the OY ratio of Upper Paleolithic Europeans to look for evidence of similarity. 2) We compare the earlier modern humans associated with the Middle Paleolithic of Western Asia with contemporary Middle Paleolithic Western Asian Neandertals to further assess the relative contributions of phylogeny and culture to adult survivorship. 3) We compare Neandertals of Western Asia with European Neandertals to address these issues and also the potential role of ecology as a contributing factor in OY ratio variation.

We examine the death distributions for changes in the relative number of adults who lived to be old, rather than for changes in the life span older adults attained, because this provides the best evidence for selection favoring the survivorship of older adults. While OY is not the ratio of older to younger adults that would be expected in living populations (Deevey, 1947), it does reflect it. There is a nonlinear relationship between dead and living OY ratios. OY ratios of the dead diverge from the living to a greater degree as OY values increase, yet there is a clear pattern of tracking between the OY ratios of the dead and the living. Therefore, observable changes in OY ratios provide some insight into the evolution of age structure in the human fossil record.

MATERIALS AND METHODS

Samples

The Middle Paleolithic hominids from Western Asia (Tabun, Skhul, Qafzeh, Amud, Kebara, and Shanidar)

[1]In this paper, we refer to non-Neandertal Middle Paleolithic hominids as "modern humans," recognizing that this term is controversial. Definitions of modernity are complex, and "modern humans" may not represent a distinct taxonomic entity. Nevertheless, it is conventional to use this term to refer to non-Neandertal Middle Paleolithic specimens from West Asia, and we employ it here.

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TABLE 1. Samples[1]

	Old	Young	Total	OY
West Asian Neandertals	9	9	18	1.00
West Asian early modern humans	6	8	14	0.75
European Neandertals	36	103	139	0.35
European modern humans (UP)	88	42	130	2.10

[1] Sample sizes and older/younger adult ratios (OY) for samples used in this study. While we recognize that early non-Neandertals are different in many respects from living modern humans, for lack of a better term, we refer to individuals from Skhul and Qafzeh as "early modern humans." Further details are discussed in text. UP, Upper Paleolithic.

comprise the most appropriate sample for discriminating between the phylogenetic and cultural influences on adult survivorship in the European Upper Paleolithic, because West Asian Middle Paleolithic populations include both Neandertals and non-Neandertals (early modern humans). This sample provides the opportunity to compare biologically different groups that manifest the same cultural complexity. These two groups, recognized by many scholars as taxonomically distinct, were roughly contemporaneous, and are associated with the same material cultural remains and other reflections of marked behavioral similarity. Moreover, given their temporal placement and geographic situation between Europe and Africa, where even earlier moderns such as Herto have been found (White et al., 2003), the early modern humans of Western Asia potentially represent populations ancestral to later modern humans in Europe. Since their designation as "Proto-Cro-Magnons," there has been a long literature from various, often opposing, perspectives suggesting that West Asian moderns are among the ancestors of modern humans in Europe (Bar-Yosef and Vandermeersch, 1993; Klein, 1999; Wolpoff et al., 2001). Moreover, the West Asian sample of modern humans is the only sample of potential ancestors for Upper Paleolithic Europeans large enough to analyze. For these reasons, the West Asian samples are uniquely appropriate for examining the double question of whether high adult survivorship was established in potential ancestors of modern humans before they appeared in Europe, and whether this was an attribute of modern humans as a taxon, rather than an attribute of the Upper Paleolithic. Although the West Asian sample is smaller than the samples used in our initial study (Caspari and Lee, 2004), it represents the only direct way to address this important issue and its analysis may suggest working hypotheses to account for the large increase in adult survivorship seen in Upper Paleolithic Europeans. Below, we discuss the influence of sample size on our results.

We tested the null hypothesis of no difference in OY ratios among the fossil groups listed in Table 1. Of these comparisons, those between West Asian Neandertals and early moderns, and between West Asian and European moderns, discriminate between phylogenetic and non-phylogenetic causes of variation in adult survivorship. These are detailed in Table 2. Two potential results would not refute, and could potentially support, the idea that the increased longevity of the Upper Paleolithic was a biological attribute of modern humans (Table 2). First, similar OY ratios between the earlier Middle Paleolithic and later Upper Paleolithic moderns could be used to support the hypothesis that greater longevity was a characteristic of modern humans as a species. Second, significantly higher OY ratios in West Asian early moderns compared to the culturally similar, contemporary Neandertals in the same region could suggest that differences in their adult survivorship was a modern human, rather than an Upper Paleolithic attribute. Put another way, failure to refute the null hypothesis for the first comparison could support a phylogenetic explanation for the similarity in OY ratios. In the second case, failure to refute the null hypothesis does not support a phylogenetic explanation for the increase in longevity; instead, it would be grounds for rejection of the phylogenetic explanation. A third comparison indirectly addresses the role of phylogeny as a cause of OY ratio variation. Failure to refute the null hypothesis for the comparison of Neandertals of Western Asia and Europe is compatible with the notion that the pattern of Neandertal survivorship was an attribute of their lineage rather than a reflection of ecology or environment.

Categorical age assessment

We tested the null hypothesis of no difference in the ratio of older to younger adults (OY ratio) among the groups in Table 1: Middle Paleolithic Neandertals from Western Asia, Middle Paleolithic early modern humans from Western Asia, Neandertals from Europe, and Upper Paleolithic modern humans from Europe. We chose specimens for whom we had reasonable confidence in both their categorical age assessment and in the likelihood that they each represented a unique individual.

Following our published procedures (Caspari and Lee, 2004), dental age estimates based on wear seriation (Miles, 1963, 2001; Mann, 1975; Lovejoy, 1985; Nowell, 1978; Wolpoff, 1979) and the eruption schedule of Brown et al. (1978), modified to reflect earlier M3 eruption in Neandertals (Wolpoff, 1979, 1999; Ramirez Rozzi and Bermudez de Castro, 2004), were used to place specimens into categories of older or younger adults. The age of M3 eruption signified adulthood, and individuals double the age of M3 eruption were considered older adults, i.e., the age at which one could potentially become a grandparent. Using this method, rates of wear were estimated by observing the degree of molar wear at the time of occlusal eruption of subsequent molars on immature specimens, and these were then extrapolated to older individuals. Since our assessments are categorical (older or younger adult) and not composed of age estimates themselves, our analysis does not require that the ages have an extremely high level of resolution. Error associated with category designation is much lower than that associated with age estimation, which translates into higher certainty for the results of categorical analysis. The construction of our categories and our methods of analysis circumvent potential problems posed by possible differences in eruption schedule, maturation rates, and wear rates between groups and tooth classes (Caspari and Lee, 2004; Eveleth and Tanner, 1976; Lucy et al., 1995; Mays, 2002; Molnar, 1971; Miles, 2001; Skinner, 1997).

Assessment of significance

The resulting OY ratios and sample sizes are given in Table 1. The significance of differences among OY ratios was assessed by establishing the probability of finding the observed OY ratio of one fossil group within distributions of OY ratios sampled from others. These distributions were generated through random resampling with

TABLE 2. Implications of potential results: can phylogeny, culture, or environment account for significant difference in OY ratios between different hominid groups?[1]

Comparisons		Factors that could account for significant difference	Factors that could account for absence of significant difference
West Asian early moderns (MP)	European moderns (UP)	Phylogeny: no Culture: yes Environment: yes	Phylogeny: yes Culture: no Environment: no
West Asian early moderns (MP)	West Asian Neandertals (MP)	Phylogeny: yes Culture: no Environment: no	Phylogeny: no Culture: yes Environment: yes
West Asian Neandertals (MP)	European Neandertals (MP)	Phylogeny: no Culture: no Environment: yes	Phylogeny: yes Culture: yes Environment: no

[1] Refutation of the null hypothesis of no significant difference in OY ratios between groups has different implications for various potential causes of OY ratio difference. Represented are two taxa, Neandertals and moderns; two material cultures, Middle Paleolithic (MP) and Upper Paleolithic (UP); and two environments, West Asia and Europe. Comparisons are between European moderns associated with UP, West Asian moderns associated with MP, European Neandertals (MP), and West Asian Neandertals (MP). Significant difference in OY ratios between West Asian moderns and Neandertals would support a phylogenetic explanation for difference, but between other groups would suggest cultural or other nonphylogenetic (environmental) explanations. Chart lists whether each factor (phylogeny, material culture, and environment) *could* account for either the significant difference in OY ratio between each comparison, or the absence of significant difference between them. Further details are discussed in text.

replacement. The approach of data-resampling provides a way to solve problems that lie outside the analytical boundaries of classical statistics (Efron and Tibshirani, 1993), e.g., using ratios as the statistic of interest, as in this study. Resampling also addresses the problem of interdependence of data within the death distribution, and the potential further dependence of later samples on earlier ones because of evolutionary change.

As in our previous study, the null hypothesis that there is no difference in OY ratios among the different hominid groups can be stated as a question of probability: how likely is it to observe an OY ratio of a particular hominid group in another group of interest? When the test group's OY ratio was smaller than that of the resampled group, we rejected the null hypothesis if a ratio the same as or lower than the observed OY ratio was found, on average, in 5% or less of the distribution generated from the comparative group. When the test group's OY ratio was larger than that of the resampled group, we rejected the null hypothesis if, on average, 5% or less of the distribution was the same as or greater than the observed OY ratio. Thus, for example, we tested the prediction that there is a significant difference in longevity between West Asian early moderns (OY = 0.75) and European Upper Paleolithic moderns (OY = 2.10) by assessing the probability of observing the West Asian early modern OY ratio in a European Upper Paleolithic sample of the same size (n = 14). We generated a distribution of ratios from the Upper Paleolithic sample (Fig. 1), each ratio in the distribution representing a dental sample of the same size as the observed West Asian modern group. We randomly drew 14 individuals with replacement from the Upper Paleolithic, generating an OY ratio based on that run. This was repeated 10,000 times, producing a distribution of ratios. The probability of drawing 0.75 (the observed West Asian modern OY ratio) or lower from this distribution was then assessed.

We were concerned about the impact the very small West Asian sample sizes would have on our results. While there are several approaches that could be used to quantify the uncertainty of our results, we chose a method that best preserved the already small sample. To assess the role of small sample size on the distributions,

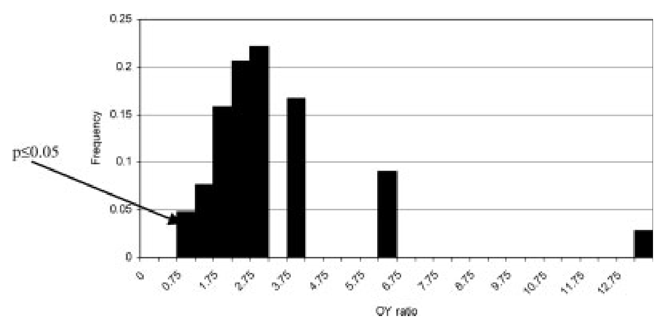

Fig. 1. Probability of finding the observed West Asian modern OY ratio (arrow at 0.75) or lower in a distribution of OY ratios generated from Upper Paleolithic Europeans by resampling. Each OY ratio in the distribution is created by randomly drawing an Upper Paleolithic sample of the same size as the West Asian modern sample, and calculating ratio of older to younger adults in it (sample sizes are shown in Table 2). This was done 10,000 times, and the generated samples describe the probability of observing the West Asian modern OY ratio or lower in the Upper Paleolithic moderns. Each one of 10,000 OY ratios is a random sample of 14 Upper Paleolithic moderns, since the actual West Asian modern sample size is 14. The probability of observing an OY ratio of West Asian modern humans (0.75) or less in the Upper Paleolithic sample is low ($\leq$0.05). To assess the influence of small sample size, this procedure was repeated 1,000 times for each of the three comparisons. Distributions of probabilities are shown in Figures 2–4.

the resampling procedure discussed above was repeated 1,000 times, and the distribution of probabilities was reported for each of the three comparisons (Figs. 2–4). The average probabilities and their 95% confidence intervals are listed in Table 3; the null hypothesis was rejected if the average probability was $\leq$5% ($P \leq 0.05$).

RESULTS

The three main comparisons, between European and West Asian moderns, between West Asian Neandertals and moderns, and between European and West Asian Neandertals, yielded markedly different results. First,

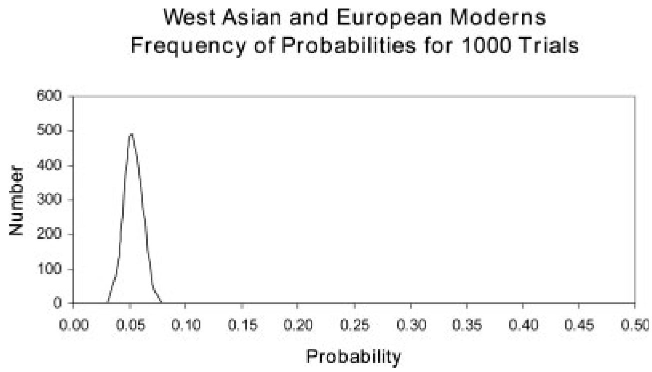

Fig. 2. Distribution of probabilities generated by 1,000 repetitions of the resampling technique outlined in Figure 1. Each of the 1,000 probabilities represents the chance of observing the West Asian modern OY ratio of 0.75 or lower in a sample of 14 Upper Paleolithic modern Europeans. Average probability is 0.05; 95% confidence interval lies between 0.04–0.07.

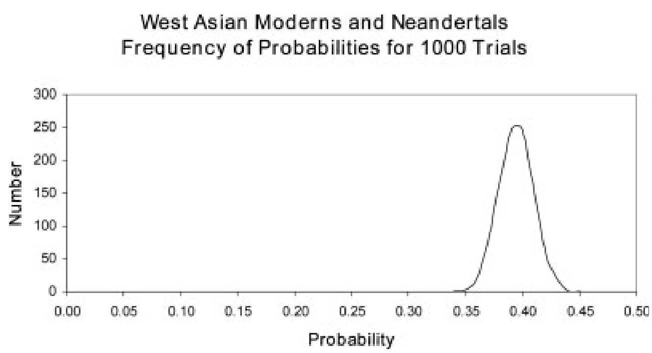

Fig. 3. Distribution of probabilities of observing the West Asian modern OY ratio of 0.75 or higher in a sample of 14 West Asian Neandertals (OY = 1.00). Average probability is 0.39; 95% of the distribution lies between 0.37–0.43. OY ratios of the two samples are not different.

the difference between OY ratios of modern humans of the Middle and Upper Paleolithic is large, and our results indicate that it is significant. The Upper Paleolithic OY ratio of 2.10 is more than double that of the Middle Paleolithic West Asian early moderns, and the average probability of observing the West Asian modern OY ratio of 0.75 or lower in the distribution of OY ratios generated from the Upper Paleolithic sample is 0.05, with a 95% confidence range from 0.04–0.07. The distribution of probabilities based on 1,000 resampling runs is shown in Figure 2. This suggests that factors other than phylogeny account for the marked increase in OY ratios in the later Europeans.

In contrast, there is no significant difference between the Neandertals and early modern humans of Western Asia (Fig. 3, Table 3). In the range of OY ratios generated from 1,000 sampling runs, each with a sample size of 14, ratios 0.75 or lower (the observed West Asian modern ratio) are in 39% of the distribution, on average. The 95% confidence interval is 0.37–0.43; none of the 1,000 generated distributions indicated a significant difference in OY ratios between the two samples. This further undermines the idea that phylogeny is directly related to differences in adult survivorship in these hominids.

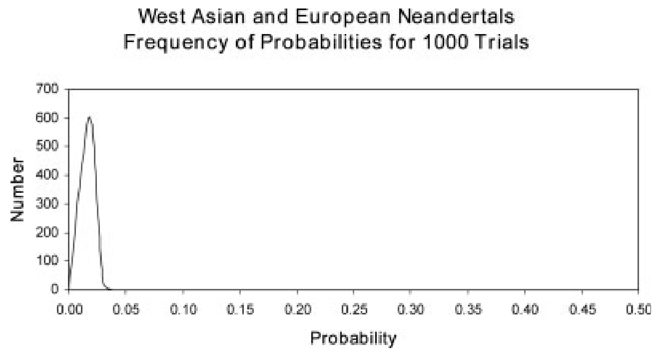

Fig. 4. Distribution of probabilities of observing the West Asian Neandertal OY ratio of 1.00 or higher in sample of 18 European Neandertals (OY = 0.35). Mean probability is under 0.02 (0.016); 95% confidence interval ranges from 0.01–0.02. All values for 1,000 trials are under 0.05, indicating significant difference in OY ratios between the two Neandertal samples.

Interestingly, however, the OY ratio of the West Asian Neandertals is significantly higher than that of the European Neandertals, also associated with the Middle Paleolithic: the average probability of observing the West Asian Neandertal OY ratio of 1.0 or greater in the European Neandertal sample is less than 0.02. (Fig. 4, Table 3); the 95% confidence interval of probabilities ranges from 0.01–0.02. This result, like the comparison of European and West Asian moderns, does not support phylogenetic explanations for OY ratio differences. However, since different OY ratios are associated with the two Middle Paleolithic groups, this result also undermines a simple cultural explanation.

DISCUSSION

The results of this study suggest that the increase in longevity associated with the modern Europeans of the Upper Paleolithic is not an attribute of modern humans as a taxon. The difference in OY ratios between the two groups of modern humans supports a nonphylogenetic explanation for the Upper Paleolithic increase in adult survivorship. The lack of significant difference between the OY ratios of Neandertals and early moderns in West Asia further suggests that the variation in adult survivorship is not the result of phylogenetic differences between groups. Moreover, the dramatic difference in OY ratios between European and West Asian Neandertal groups similarly implies that cultural, adaptive, or ecological variations rather than biology are responsible for the longevity differences.

The variation in OY ratios among Middle Paleolithic groups also suggests complexity in the relationship between material cultural traditions and longevity. Compared to European Neandertals, the West Asian Neandertals exhibit significantly greater adult survivorship, although they are associated with similar material remains. The role of differences in climate, ecology, and behavior may be reflected in the significant difference in adult survivorship between the Neandertals of Western Asia and of glaciated Europe, but phylogeny is not. The variation may be a consequence of human adaptation to climate and ecology, with more favorable conditions promoting improved adult survivorship in West Asia.

If the more temperate climatic conditions associated with Western Asia at that time account for the increased

TABLE 3. Significance of differences between OY ratios of fossil groups[1]

Comparisons		Significant difference? (average probability)	95% confidence interval
West Asian early moderns	European moderns (UP)	Yes: $P \leq 0.05$	0.04–0.07
West Asian early moderns	West Asian Neandertals	No: $P \leq 0.39$	0.37–0.43
West Asian Neandertals	European Neandertals	Yes: $P \leq 0.02$ (0.016)	0.01–0.02

[1] Reported are average probabilities (and confidence intervals) of finding the OY ratio of one group in distributions generated from another. Differences between West Asian Middle Paleolithic groups are not significant, while West Asian groups differ significantly from both European Neandertals and modern humans of European Upper Paleolithic (UP).

adult survivorship in Middle Paleolithic populations there, the high Upper Paleolithic OY ratio is even more impressive, because the climatic explanation is not possible for glacial Europe. Upper Paleolithic longevity is more than twice as common as that of the West Asian early moderns, despite the climatic extremes of the glacial maximum, and represents a fivefold increase compared to European Neandertal OY ratios. We suggest that these findings indicate cultural factors promoting the survivorship of older adults, whose experience may have benefited their kin groups in the harsh conditions of Upper Pleistocene Europe. These experiences may also underlie the material expressions associated with the Upper Paleolithic. The European Upper Paleolithic is known for a large increase in the occurrence of undisputed evidence for cultural complexity and symbolic behavior, including an increase in exotic raw materials, elaborate grave goods, body ornamentation, and representational art. Longevity may contribute to the development of these cultural trends in several interrelated ways (Rosenberg, 2004). It promotes the transgenerational accumulation and transfer of information that allows for complex kinship systems and other social networks that are uniquely human. In addition, it contributes to population growth and expansion by increasing both the individual fertility of people who survive longer, and also their inclusive fitness, allowing investment in grandchildren and other forms of intergenerational transfer (Lee, 2003; Hawkes, 2003; O'Connell et al., 1999). The importance of intergenerational transfer of a variety of cultural resources may underlie the shifts in mortality associated with human longevity (Lee, 2003). Therefore, we view the increase in adult survivorship in the Upper Paleolithic as a positive feedback process: initially a consequence of cultural adaptation, it became a prerequisite for the unique and complex behaviors that mark modernity, innovations which may have promoted the importance and survivorship of older adults. Increased longevity represents a link between biological and behavioral modernity, an example of the impact of culture on human biology and its role in recent human evolution.

CONCLUSIONS

This work suggests that the increase in adult survivorship associated with modern Europeans of the Upper Paleolithic is not a direct consequence of the emergence of modern humans as a taxon. However, the West Asian sample sizes are small, and further fossil finds are necessary for confirmation of the results reported here. We calculated a mean probability of only 0.05 of finding an OY ratio as low as the West Asian moderns in randomly resampled sets of 14 Upper Paleolithic Europeans, but the 95% confidence interval is large (0.04–0.07). There is no significant difference between the OY ratios of Neandertals and early moderns in West Asia, and the similarity between these two samples also discounts the role of phylogeny. Finally, variation in OY ratios between the European and West Asian Neandertal groups implies that cultural, adaptive, or ecological factors are responsible for the disparity in adult survivorship. Therefore, our working hypothesis is that the longevity pattern observed for Upper Paleolithic Europeans is probably not an attribute of modern humans as a species, and instead may reflect cultural changes in Europe after modern humans arrived there.

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