



News and Views

Taxonomy and longevity: a reply to Minichillo (2005)

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We recently used the fossil record to examine theoretical predictions that had been made about demographic age-structure changes in human evolution (Caspari and Lee, 2004). Although it had been suggested that longevity increased in early *Homo* populations based on brain size increases and other correlates of longevity, this question, and others involving changes in age structure, had not previously been addressed using the fossil record.

Our paper on adult survivorship was empirical; we were careful to make our assumptions explicit, and we were cautious in the interpretation of our results. These interpretations could be easily biased by preconceived ideas about the relationships between the groups studied, and for that reason we avoided taxonomic or phylogenetic assumptions, focusing instead on variation over time. In his commentary, Minichillo (2005) makes

suggestions that require phylogenetic assumptions that our study neither demanded nor addressed.

We tested a null hypothesis of no difference in adult survivorship by examining the ratio of older to younger adults (OY ratio) in four hominid groups, using the largest samples yet to be analyzed: later australopiths, early/middle Pleistocene *Homo*, Neandertals, and Upper Paleolithic Europeans (Caspari and Lee, 2004). Age categories were based on tooth wear. There were differences, and we assessed their significance using random resampling with replacement. We presented this analysis as a baseline study, one that was intended to provide general characteristics of age structure for several hominid groups. One of our interests was to test whether the fossil record supported a prediction arising from the work of O'Connell et al. (1999) regarding the “grandmother hypothesis,” as applied to early *Homo*. These authors suggested that a grandmother effect may have been related to the success of early *Homo erectus* populations, whose adaptation to environmental changes in the early

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Pleistocene involved expanded dietary breadth, including a significant number of tubers—a way of life in which grandmothers could have played an important economic and child-rearing role. We expected a consequence of the grandmother hypothesis to be a concomitant increase in adult survivorship in early *Homo* populations (compared to australopiths), reflecting selection for larger numbers of older adults that promoted intergenerational transfer effects (Lee, 2003). Our question, then, was simple: Was there a difference in OY ratios among the four samples, and in particular, was there an increase in early *Homo* compared to australopiths? We concluded that there was a significant difference among all four groups (Fig. 1).

We discussed two implications of our results (Caspari and Lee, 2004). First, we found that each group had a significantly higher OY ratio than temporally earlier groups. Therefore, our results *could* support (i.e., did not refute) the grandmother hypothesis as applied to early *Homo* because the early *Homo* OY ratio was significantly higher than that of the australopiths. We do not agree with Minichillo's (2005) contention that our results provide no support for O'Connell et al.'s (1999) position. However, because these OY ratios are still very low (OY = 0.25), we considered it weak support. The “weak support” Minichillo (2005: 643) refers to in his introduction—“[Caspari and

Lee] further stated that these findings weakly support the Grandmother Effect, as articulated by Hawkes and colleagues (Hawkes et al., 1998; Hawkes, 2003), as a primary difference *between modern and non-modern peoples*” (emphasis added)—actually applied to O'Connell et al.'s position. We wrote: “these findings weakly support the predictions of the grandmother hypothesis *as applied to Homo erectus*” (Caspari and Lee, 2004: 10898, emphasis added). We think our results could provide *strong* support for the grandmother effect (or an “older person effect”) as a primary difference between modern and non-modern people.

The second and more important implication of our paper involved the most recent sample, Upper Paleolithic Europeans, whose OY ratio was five times higher than that of Neandertals. We proposed that the behavioral modernity associated with the Upper Paleolithic may be linked to the increase in the number of adults who survived to older ages, and suggested ways that the Upper Paleolithic may have been a consequence of changes in demographic age structure. While we did not rule out the possibility that the change in age structure was an attribute of a modern human lineage, we also didn't assume it. In fact, we did not test hypotheses about the *cause* of changes in age structure (i.e., whether they were a consequence of lineage differences or not), and we made no taxonomic inferences.

Minichillo's (2005: 643) critique is:

Unfortunately, the that data Caspari and Lee had available failed to address the questions they would have liked them to. If the question is “Were age structures different between Upper Paleolithic *Homo sapiens* and Middle Paleolithic *Homo neanderthalensis*?” then the answer is decidedly “yes,” and stunningly so. But this is neither the question that Caspari and Lee asked nor the result that they emphasized.

To the contrary, this is precisely the question we asked of all the *Homo* groups, and the results we emphasized, but without the taxonomic emphasis that Minichillo gives.

Minichillo's comment implies that our paper focused on the modern human origins issue. If so,

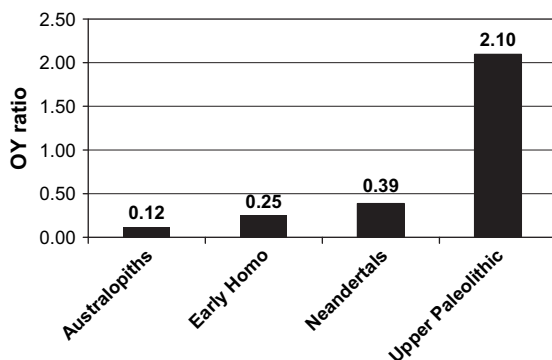


Fig. 1. Ratios of older to younger adults. Results from Caspari and Lee (2004). There is a significant increase in adult survivorship between all groups sampled, with the largest increase in the Upper Paleolithic sample.

it perhaps reflects a misunderstanding of our use of “late” in the title: “Older age becomes common late in human evolution.” “Late,” in the context of our paper, referred to the difference between early and late Pleistocene; we reported that age structure changes were more dramatic in the modern humans of the Upper Paleolithic than in our earlier samples, but these are not the earliest modern humans. We did not address the question of whether age structure changed with the *emergence* of modern humans or occurred later than that, i.e., in the Upper Paleolithic. Minichillo is interested in whether the increase in longevity is an attribute of modern humans as a taxon, but this is not the question we addressed.

Minichillo assumes a unique African ancestry for modern Europeans. Given that, it is possible to address the question he thinks we should have asked: Is the increase in OY ratios found in Upper Paleolithic Europeans an attribute of a modern human taxon, or did it arise later, perhaps associated with cultural change within modern humans? We recently tested this idea by examining whether the high OY ratio of Upper Paleolithic Europeans is present in Middle Paleolithic “modern humans,”¹ potential ancestors of the later modern humans of Europe (Caspari and Lee, 2005, *in press*). We addressed this issue using a western Asian Middle Paleolithic sample, including both Neandertals and moderns (Caspari and Lee, 2005, *in press*). We conducted two tests. First, since the two groups are both associated with the Middle Paleolithic, yet are often considered to be different species (lineages), a comparison of their OY ratios is informative. Second, since the western Asian moderns are usually considered to be closely related to earlier and contemporary modern humans in Africa, and have been viewed as ancestral to Upper Paleolithic Europeans by workers on all sides of the

modern human origins controversy (e.g., Bar-Yosef and Vandermeersch, 1993; Klein, 1999; Wolpoff et al., 2001), we compared western Asian moderns to the later Upper Paleolithic modern humans from Europe.

Our Middle Paleolithic western Asian sample is small ($n = 32$) compared to the samples in our original study. Using resampling methods to assess the impact of small sample size, we found there was no significant difference in adult survivorship between the roughly contemporary Middle Paleolithic Neandertals ($n = 18$; OY = 1.0) and modern humans ($n = 14$; OY = 0.75) in western Asia (Caspari and Lee, 2005, *in press*). The lack of age structure variation implies that phylogeny is not a factor in the large OY ratio differences between the Neandertals and modern humans in Europe. We also compared the modern humans of the Middle and Upper Paleolithic. The Upper Paleolithic Europeans had an OY ratio (2.10) that was significantly larger than that of the Middle Paleolithic moderns (0.75). This result indicates that the large increase in the European moderns is not directly related to phylogeny (Caspari and Lee, 2005, *in press*).

In conclusion, the causes of adult mortality and survivorship across the span of human evolution are complex—caused by a variety of ecological, behavioral, and possibly phylogenetic factors. However, the consequences of a reduction in young-adult mortality may be linked to demographic changes that could have influenced the behavioral expressions of the Upper Paleolithic, and the intergenerational transfers that make older individuals in social species evolutionarily important, despite their decreasing fertility (Lee, 2003; Caspari and Lee, 2004; Rosenberg, 2004). Our original work made no assumptions about potential causes, but used the fossil record to test limited questions about changes in adult survivorship that may provide insight into life history evolution. This kind of empirical approach uses the prehistoric record to test hypotheses generated from evolutionary theory, and when keeping assumptions to a minimum, provides a basis for the generation of further hypotheses about the causes and effects of life history changes over the course of human evolution.

¹ We refer to the non-Neandertal Middle Paleolithic hominids as “moderns,” although we recognize that their categorization as “modern humans” or “anatomically modern humans” is controversial. Definitions of modernity are complex, and “modern humans” may not represent a monophyletic group. Nevertheless, it is conventional to use “modern” to refer to the non-Neandertal Middle Paleolithic specimens from western Asia, and we employ it here.

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