



News and Views

How old is human longevity?

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Seeking to locate changes in longevity in hominin evolution, Caspari and Lee (2004) calculated a ratio of old to young adult dentitions in assemblages of fossil taxa. They found an especially large difference in this ratio between Neandertals and Upper Paleolithic modern humans. While the important question they addressed can only be answered with fossil evidence, their ratio, as we show here, is not a measure of longevity. If their age categorizations are correct, the ratios do show very different representations of the deaths of old and young adults in the assemblages analyzed. Instead of changes in longevity, these differences more likely reflect biases in the ages at death represented in the assemblages.

Caspari and Lee (2004: 10895) say: “Increased longevity, expressed as a number of individuals surviving to older adulthood, represents one of the ways the human life history pattern differs from other primates.” Using an analysis of tooth wear to classify fossil dentitions as young or old adults, they concluded that the longevity characteristic of modern humans first appeared in the late Pleistocene and contributed significantly to

the success of moderns relative to other hominins, notably Neandertals. We agree that changes in life history were critical to human ecology and evolution, and that fossil data provide the only direct evidence of their emergence. But the measure Caspari and Lee used to track shifts in longevity does not do so. We show this by applying their measure to a sample of modern primates with very different longevity. Comparisons between the results for living populations and Caspari and Lee’s results for fossil assemblages highlight the archaeological problem recognized by paleodemographers: skeletal assemblages do not reflect the age structure of past populations.

Caspari and Lee used the third molar (M3) to distinguish adult dentitions because the eruption of M3 marks maturity in Old World anthropoid primates (Schultz, 1956; Smith, 1989). They classified dentitions as young if M3 showed little or no wear; “old” if the degree of wear indicated “twice the age” at M3 eruption or older (Caspari and Lee, 2004: 10896). By using M3 eruption, they avoided the difficulty of estimating unknown maturation ages for the taxa represented. Twice the age at M3 eruption is the beginning of old age since that is when “one could theoretically first become a grandmother” (Caspari and Lee, 2004: 10896). Their ratios of old-to-young adults (OY)

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for samples representing four hominin taxa are 0.12 for australopiths, 0.25 for *H. erectus*, 0.39 for Neandertals, and 2.08 for Upper Paleolithic moderns. On this basis, they concluded that longevity increased across hominin taxa from Pliocene times onward, most dramatically between Neandertals and modern *H. sapiens*, when the ratio of “old” to “young” jumped by a factor of five.

These results are arresting, but they do not measure differences in longevity. Here is why: While adult life spans (both average and maximum) vary widely across the primates, as do differences in age at maturity, the two variables are closely correlated with each other (Schultz, 1956; Charnov, 1993). This ratio of average adult life span to age at maturity is approximately invariant across primate species (Charnov, 1993). In other words, all else being equal, the OY ratio should differ little, whatever the cross-species differences in longevity.

We illustrate this point by using published M3 eruption ages (Smith et al., 1994) and published life tables to calculate OY ratios for Japanese macaques (Pavelka and Fedigan, 1999), chimpanzees (Hill et al., 2001), and modern human hunter-gatherers (Howell, 1979; Hill and Hurtado, 1996; Blurton Jones et al., 2002). Table 1 shows average M3 eruption ages reported for these species and the young adult and old adult age ranges according to Caspari and Lee's definitions. Table 2 shows the proportion of young adults and old adults in the standing age structure of populations of these species estimated from life tables. This is exactly the ratio we think Caspari and Lee aimed to

Table 1
Young and old adult age classes as defined by Caspari and Lee

Species	M3 eruption (yrs) ^a	Young adult (yrs) ^b	Old adult (yrs) ^c
<i>Macaca fuscata</i>	~5	5–9	>10
<i>Pan troglodytes</i>	~10	10–19	>20
<i>Homo sapiens</i>	~20	20–39	>40

^a Data from Smith et al. (1994).

^b Defined by Caspari and Lee as age at M3 eruption to twice that age.

^c Defined by Caspari and Lee as twice the age of M3 eruption and older. In the life tables used below, the oldest age represented for *M. fuscata* is 32; for *P. troglodytes* it is 55; and for *H. sapiens* it is 84.

Table 2
Proportions of young and old adults estimated by the method of Caspari and Lee in standing populations of living species

Species	Young adults ^d	Old adults ^e	O/Y ratio ^f
<i>Macaca fuscata</i> ^a	50.8%	49.2%	0.97
<i>Pan troglodytes</i> ^b	47.8%	52.2%	1.09
<i>Homo sapiens</i> ^c	47.1%	52.9%	1.12

^a From Pavelka and Fedigan (1999).

^b From Hill et al.'s (2001) synthetic life table for five wild chimpanzee populations.

^c The average from three hunter-gatherer populations: Howell (1979), Hill and Hurtado (1996), and Blurton Jones et al. (2002).

^d Calculated from the life tables cited. A life table indicates the number of individuals surviving from an initial birth cohort to reach each age in the life span. When populations are stationary, the age pyramid mirrors this survival schedule. We assumed that the cited life tables represent stationary populations and therefore represent the standing age distribution of each species. Caspari and Lee defined young adults as those between the age at M3 eruption and twice that age. To calculate the proportion of the adults that are young, we did the following: sum the numbers surviving at each age through young adulthood and divide that by the sum of the numbers surviving at each age through all adulthood.

^e The old adults are all the adults minus the young adults.

^f This ratio is the proportion of old adults divided by the proportion of young adults.

estimate for the fossil taxa. The OY ratios for the living populations are 0.97, 1.09, and 1.12, respectively. Macaques, chimpanzees, and humans all have very different longevities, but they all have different ages at maturity as well. Since ages at M3 eruption scale with average adult life spans, differences in OY ratios are negligible—approximately invariant. Even if longevity differences among past hominins were as great as those between monkeys and modern humans, an OY metric that actually tracked population age structure would show much less variation than they report. The differences Caspari and Lee found in this measure of their fossil assemblages indicate something other than differences in longevity.

Like Caspari and Lee (2004), many analysts have used age distributions in archaeological skeletal assemblages to address questions of ancient population age structure (recent examples include Trinkaus and Tompkins, 1990; Trinkaus, 1995; Kennedy, 2003; Bermudez de Castro et al., 2004). The implicit assumption is that the age

distribution of deaths in the assemblage reflects the age distribution of deaths in the population it samples. But paleodemographers have repeatedly shown that this assumption does not hold (for argument and supporting data, see Wolpoff, 1979; Howell, 1982; Boquet-Appel and Masset, 1982; Walker et al., 1988; Konigsberg and Frankenberg, 1994; Aykroyd et al., 1999; Hoppa and Vaupel, 2002; Hawkes and Blurton Jones, 2005). There are three main reasons for this fact: 1) ages of adults are systematically misestimated (e.g., Boquet-Appel and Masset, 1982; Aykroyd et al., 1999); 2) while techniques have been developed to reduce this bias (Hoppa and Vaupel, 2002), the bones of older individuals are less likely to be preserved (e.g., Walker et al., 1988); and 3) perhaps most important, even if these two biases were corrected, archaeological assemblages will only reflect the mortality experience of populations if they randomly sample deaths at each age (e.g., Konigsberg and Frankenberg, 1994).

Although Caspari and Lee (2004: 10896) did not identify their individual specimens, they used the Miles method to categorize them: “rates of wear are estimated by observing the degree of molar wear at the time of occlusal eruption of subsequent molars on immature specimens and these rates are then extrapolated to older individuals.” In principle, this method should take account of differences in diet and associated wear rates in different populations. But even for modern human assemblages, there is some art in the process (Miles, 2001). When applied to non-modern taxa, not only must wear rates be estimated, but also time before and between molar eruptions. The possibility of age misestimation is not negligible. Even if we accept Caspari and Lee’s age categorizations, the preservation bias against the bones of older individuals means that assemblages from the deeper past should contain disproportionately fewer intact dentitions from older adults, even if they were initially deposited in equal proportions. Some of the very low values for older adults Caspari and Lee found among pre-modern taxa may mark the effect of time’s arrow.

In the case of Upper Paleolithic moderns, however, they find just the reverse: relatively more older adult deaths than in populations of modern

hunter-gatherers. Caspari and Lee (2004: 10895) say that while their ratio is “not the OY ratio that would be expected in the living populations (Deevey, 1947), it does reflect it.” But the ratio would only reflect the relative rates of death for old and young adults in the population if the deaths represent “a large and reasonably random sample of the population” (Deevey, 1947: 288), i.e., if deaths at different ages were equally likely to be represented in the archaeological assemblages. The wide variation in the value of the OY ratios indicates that this requirement has not been met.

Regular demographic processes determine the age structure of living populations. When age-specific rates of fertility and mortality persist over a few generations, populations of any species reach a stable age distribution (Lotka, 1922; Charlesworth, 1994). A stable population grows (or declines) at a constant rate, but the fraction of the population in each age class remains unchanged. Because population growth rates are exponential, they cannot depart very far from zero for any length of time. Charnov’s (1993) model explaining the invariant relationship between average adult life span and age at maturity in mammals is based on this demographic foundation. In any population that maintains itself over time, the rate at which adults die cannot be greater than the rate at which individuals mature to adulthood.

Each of the taxa Caspari and Lee investigated persisted over many hundreds of generations, and each is part of the Old World anthropoid clade. Stable population theory and the similar fractions of relatively old to young adults in living primate populations are grounds for hypothesizing similar ratios in the standing age distribution of those populations when they were extant. On those grounds, Caspari and Lee’s OY ratios do not measure differences in longevity, but instead index bias in the representation of deaths for age category in their samples. Some of that bias may be due to age misestimation, some to the differential preservation of the bones of older adults in more recent assemblages. But more generally, even large death assemblages need not represent the mortality experience of populations. Individuals of different ages and sexes may tend to die in different places, and/or be treated in different ways at death. Caspari

and Lee (2004: 10895) noted that longevity in past hominins has mostly been “discussed through its correlation with other variables, such as body size, encephalization, and growth and development patterns.” One reason for focusing on variables that can be measured on a few individual specimens is the lesson (or curse) of paleodemography: archaeological death assemblages do not reflect the age-specific mortality of the populations that left them. That makes reading life histories in the skeletal data a continuing challenge. Theoretically guided research on the variation in living populations provides crucial tools for the job.

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