Commentary

Genetics, archaeology, and Holocene hunter-gatherers

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Excoffier and Schneider’s (1) analysis of mtDNA diversity in a large sample of modern human populations yields results consistent with those of previous work, indicating a series of sharp expansions in human population size during the early Upper Pleistocene [50–100 thousand years ago (KY)]. These expansions perhaps originated first in Africa and then proceeded stepwise across Asia and the Americas and later into Europe. Surprisingly, however, not all populations in Excoffier and Schneider’s (1) sample show evidence of these expansions; the exceptions include several Native American and hunter-gatherer groups. These are explained by appeal to recent or recurrent population crashes or other processes likely to have eliminated genetic evidence of earlier growth. Especially provocative is the suggestion that recent hunter-gatherer populations as a class may be smaller and more isolated than their Pleistocene predecessors and thus more prone to demographic upset. The utility of such populations as models for the analysis of human demography in the Pleistocene is drawn into question accordingly.

**Genetic vs. Archaeological Evidence of Ancient Population Growth.** If Excoffier and Schneider (1) are right about early Upper Pleistocene population increases, then the archaeological record should offer some support, possibly including indications of any behavioral changes that might have facilitated such growth, certainly by providing evidence of population increases themselves (e.g., more sites, higher rates of refuse deposition, and more colonization of areas previously unoccupied). As it happens, the anticipated matches are mixed at best; major changes in the archaeological record generally trail the dates proposed by Excoffier and Schneider (1) and others, sometimes by tens of millennia. The correlation is best in Africa, Europe, and parts of Asia, where the first appearance of the Upper Paleolithic—complete with evidence of art, formal burial, and other indications of modern human behavioral capabilities—is generally dated at about 35–50 KY. These dates overlap the more recent ends of the 95% confidence intervals bracketing the proposed period of population growth, although they fall short of many of the mean \( \tau \) values, particularly in Africa (2). The same is true for Australia/New Guinea, where the earliest archaeological dates are in the range 40–60 KY (3), again overlapping the upper end of the 95% confidence interval but falling well short of three of four mean \( \tau \) estimates cited for this region (76–97 KY). The mismatch is most striking in the Americas. There, dates for two indigenous populations showing what Excoffier and Schneider (1) take to be clear indications of Pleistocene expansions are 55 and 59 KY (confidence intervals of 26–99 and 28–82 KY, respectively); however, the earliest generally accepted archaeological dates are no greater than 13 KY (4, 5), Excoffier and Schneider’s (1) assertions about the existence and reliability of 30–35 KY dates notwithstanding (6).

These discrepancies may mean that (i) the accumulation of recognizable archaeological evidence for population expansions often trailed the expansions themselves by very substantial lengths of time; (ii) the estimated mtDNA mutation rate is too low, making the genetically based dates for expansions too early; or (iii) dates for population expansion in what are now identified as non-African lineages may be unrelated to those for the colonization of other continents. The first of these possibilities seems unlikely, especially given the size of the growth spurts posited by geneticists. Events of this magnitude should have fairly clear and immediate archaeological consequences. The idea that the mutation rate might be pegged too low seems a stronger possibility. Excoffier and Schneider’s (1) reasons for rejecting this idea, notably that dates for mitochondrial Eve would have to be adjusted forward, are not entirely compelling. The third alternative, that population expansions might have begun well before continental colonizations, seems quite likely, particularly for Australia/New Guinea and the Americas. Both could have been occupied by multiple groups that had already diversified elsewhere well before entering either of these regions.

**Genetic Diversity Not Explained by Stepwise Expansions.** Excoffier and Schneider’s (1) suggestion that the absence of evidence for Pleistocene population growth in some modern groups is a reflection of recent demographic upset seems quite plausible. The wonder is that such upsets have not disrupted the genetic record of ancient demographic change more thoroughly. Excoffier and Schneider (1) cite the catastrophic impact of European colonization on certain Native American populations. In fact, its effects were widespread on a continental scale, not only in the Americas (7, 8) but elsewhere (9).

Relatively recent climatic changes may also have had important demographic consequences, especially at the Pleistocene/Holocene boundary (10–15 KY), when mean annual temperatures worldwide rose and fell repeatedly over ranges \( \approx 5^\circ C \) across periods of less than a century, sometimes less than a decade (10, 11). It is not hard to imagine that human populations everywhere suffered greatly as a result, reinforcing the notion that the growth spurts indicated for many of those included in the sample of Excoffier and Schneider (1) might have occurred much later than many geneticists think and again raising questions about the assumed mtDNA mutation rate. Perhaps the idea that at least some were terminal (rather than early Upper) Pleistocene phenomena is not far-fetched.

**Recent Hunter-Gatherer Populations as Analogues for the Pleistocene.** The notion that historic and modern foragers, like the !Kung, can be taken as Pleistocene relics has been challenged repeatedly by anthropologists over the past 3 decades, and for good reasons. Most live in relatively unproductive habitats, some of which were unoccupied before the end of the last glaciation. Many are surrounded by agriculturists. Some are embedded in large, state-level political systems of a kind that have existed for no more than a few thousand years (12).

That said, it would be a mistake to infer, following Excoffier and Schneider (1), that, as a class, historic and modern foragers are genetically more isolated and that their effective population sizes are thus necessarily smaller than those of their Pleistocene predecessors. All historic and modern hunter-
gatherers have different, generally more complex extractive technologies than did Pleistocene foragers. Most historic and modern foragers exploit much broader arrays of resources, and some have markedly higher local population densities, especially from the mid-Holocene onward. A few occupied very productive habitats, notably in parts of the Americas (12–14). Genetic, ethnographic, and archaeological data indicate that those hunter-gatherers with agricultural neighbors interacted reproductively with them over long periods, probably from the time the groups first came into contact (15–17). Moreover, at least some historic and modern foragers have moved repeatedly between farming and foraging lifestyles within the last few millennia (17). Those without farming neighbors (and there were many across all of Australia and over very large parts of the Americas) had equally extensive contact with surrounding hunter-gatherer groups (14, 18–20).

In short, it is hard to see recent hunter-gatherers overall as either genetically more isolated or demographically more fragile than those of the Pleistocene simply as a function of the spread of agriculture. Abandoning them as a source of demographic insight on the distant past seems premature. It is better to assess the utility of each population as a potential analogue independently rather than to accept or reject them all categorically.

Excoffier and Schneider’s (1) analysis is important in that it helps move genetic research on recent human evolution away from the “African Eve vs. multiregional origins” argument that has dominated the literature over the last decade toward a broader and, in many ways, more interesting set of questions. The techniques they deploy clearly have enormous positive potential. Fully realizing that potential will require active collaboration between geneticists and their colleagues in the historical sciences, especially anthropology.