COMMENTARY

Prehistoric hunter–gatherer population growth rates rival those of agriculturalists

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Among the many useful yardsticks of evolutionary success, trajectory of population growth is perhaps the most telling, and it is the focus on this metric that makes the contribution by Zahid et al. (1) in PNAS so compelling. They document hunter–gatherer population growth between 13,000 and 6,000 y ago in the western US states of Wyoming and Colorado, in doing so showing (*i*) that reliable population trajectories can be obtained through careful analysis of the radiocarbon record, and (*ii*) that the Wyoming-Colorado hunter–gatherers they studied achieved long-term rates of population growth comparable to the rates of population growth achieved by prehistoric New and Old World agriculturalists, and (*iii*) they proceed on the basis of this and other evidence to generalize that contrary to received wisdom, prehistoric hunter–gatherers consistently achieved long-term growth rates equivalent to the growth rates of prehistoric agriculturalists. These findings raise a multitude of interesting questions regarding the transition from hunting and gathering to agriculture, particularly why, without enjoying any competitive advantage in rate of population growth, agriculture was so consistently able replace hunting and gathering worldwide during the Holocene.

The basis for the argument rests on the analysis of a large suite of radiocarbon dates (n = 7,900) from Wyoming and Colorado that have been calibrated (Fig. 1*A*) and then merged into a single record in the form of what is termed a summed probability distribution (Fig. 1*B*). The procedure begins with individual radiocarbon dates, each representing a range of dates with a given mean and SD of probability. Because the concentration of atmospheric radiocarbon has varied historically, this probability distribution must be corrected, or calibrated, using the empirically observed correspondence between radiocarbon dates and calendar dates (2, 3), producing a probability distribution in calendar years before present (cal BP). Zahid et al. (1) summed these probabilities for their entire Wyoming-Colorado radiocarbon sample on the assumption that when corrected for differential preservation (4), years with higher summed probabilities would correspond to years with higher population densities.

Although it is unclear at what point one should regard a radiocarbon sample as representative of population size, the one between 13,000 and 6,000 cal BP analyzed by Zahid et al. (1) would seem to qualify because it reveals a pattern so temporally persistent that it is unlikely due to sampling error or bias. It suggests a trajectory of continuous, long-term Wyoming-Colorado hunter–gatherer population growth of 0.041% from 13,000–6,000 cal BP, doubling roughly every 1,700 y, within which there were short-term fluctuations during which growth rates were sometimes more than an order of magnitude larger (i.e., $r > 0.4\%$), doubling in less than 200 y. Spanning the transition from a highly mobile, large-game–focused Paleoindian adaptation to a less mobile Archaic adaptation that made greater use of small game and plants (5), the long-term Wyoming-Colorado rate is broadly consistent with radiocarbon estimates for North America overall [i.e., including both hunter–gatherers and agriculturalists and bridging from one to the other (6)], almost exclusively hunter–gatherers in Australia (7), European agriculturalists (8), and prehistoric population worldwide (9). That the rates of population growth indicated by these studies are so consistent with each other has important theoretical implications.

Most obviously, that agriculturalists in North America, Europe, and elsewhere grow no faster than, and Australian hunter–gatherers grow just as fast as, Wyoming-Colorado hunter–gatherers between 13,000 and 6,000 cal BP suggests that the differences in adaptation, environment, and time separating these groups are less influential determinants of population growth, thus perhaps less evolutionarily important, than once thought. For example, mobility has traditionally been argued to limit hunter–gatherer fertility on the logic that because mothers could only carry one child, the minimum space between births among mobile populations would be determined by the age at which a child could walk on its own when a family moved from one camp to another, a premise central to the thesis that mobility had limited Pleistocene hunter–gatherer population growth and the emergence of sedentism in the early Holocene had triggered major post-Pleistocene

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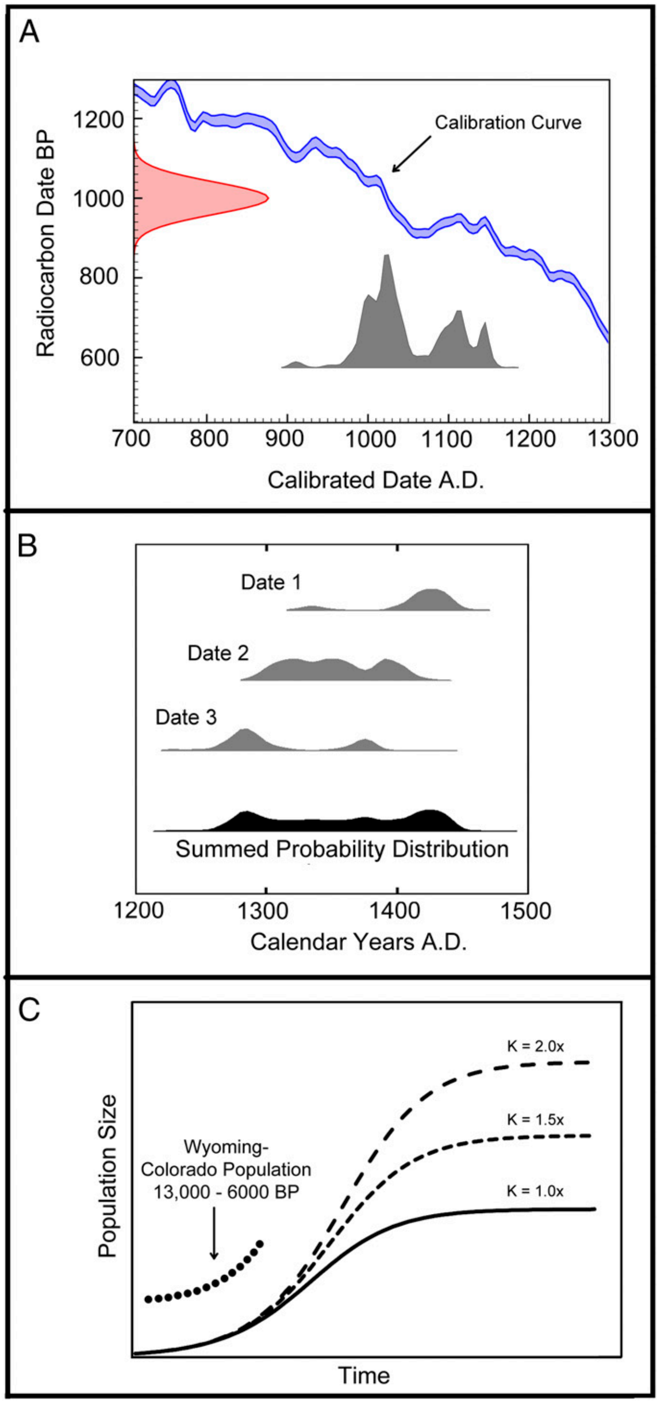

Fig. 1. (*A*) Individual radiocarbon date with a given mean and SD of error, represented by the normal curve plotted in red on the *y* axis at the left, is matched against the calibration curve, plotted as a blue band running from the upper left to lower right, to obtain a calibrated date, given by the intersection of the radiocarbon date with the calibration curve, shown by the probability distribution in gray at the bottom. (*B*) Probabilities of three calibrated radiocarbon dates are summed and normalized to obtain a summed probability distribution (SPD). (*C*) Three logistic growth curves depicting populations with identical intrinsic growth rates but different carrying capacities. The Wyoming-Colorado growth curve 13,000–6,000 cal BP, shown on the left, is the growth curve of a population unaffected by carrying capacity. (*A* and *B*) Both figures were redrafted from figures obtained using OxCal version 4.2.4 (2) and calibrated using an IntCal 13 atmospheric curve (3).

population growth leading to the development of agriculture (10). This traditional understanding seems not to be true. The major trend from more to less mobile settlement patterns during the Holocene seems to have had little or no effect on population growth rates demonstrated in radiocarbon records, the Wyoming-Colorado record in particular, which spans the shift from more mobile Paleoindian to less mobile Archaic adaptations, lending support to the idea that mobility, per se, does not inhibit fertility (11).

If mobile hunter–gatherer populations can grow as fast as sedentary agriculturalists, what accounts for the steadily increasing advance of agriculture at the expense of hunting and gathering? One must first note that replacement was not universal; hunter–gatherers maintained a major presence in the western United States, in California and the Northwest Coast in particular, and made major advances against agriculturalists in the US Great Basin and Southwest (12), for example. Such exceptions notwithstanding, the Holocene dominance of agriculture overall is clear, and certainly due to differences in carrying capacity, *K*, which determines how large a population can grow, as given by the usual equation tracking growth of population size, *N*, as it changes per unit of time, *t*, given an intrinsic growth rate, *r*:

$$\frac{dN}{dt} = rN \cdot \left(1 - \frac{N}{K}\right). \qquad [1]$$

Populations responding to this combination of forces will demonstrate the classic S-shaped logistical growth curve, growing slowly initially because a population is small to begin with, gradually increasing to a maximum as a population grows larger, increasing the effect of *r*, and then slowing and eventually halting altogether as a population reaches carrying capacity (i.e., $N = K$) (Fig. 1*C*). Carrying capacity can be difficult to calculate, but it varies strongly with the density and growth rate, *r*, of limiting resources (13), both of which are much higher for plants than for animals and much higher for domesticated plants than for wild plants. As populations grow large, evolution favors adaptations that maximize energy use per unit of space despite the growing costs of procurement and processing that go with such adjustments (12). In this view, the Wyoming-Colorado populations 13,000–6,000 cal BP, as well as other populations with nondecreasing growth rates reported in studies mentioned by Zahid et al. (1), reflect the initial part of the logistic curve, before populations have grown large enough to be affected by carrying capacity (Fig. 1*C*). That hunter–gatherer populations grow just as fast as agriculturali populations likely explains the failure of agriculture to develop and spread in the Pleistocene, when climate varied so rapidly that populations never reached carrying capacity (14), giving agriculture no advantage until the Holocene, when climate stabilized dramatically. In sum, for the most part, preindustrial populations, both hunter–gatherer and agriculturalist, seem to have grown at the same rate, no matter what was eaten or how it was obtained, provided only that there was enough of it.

A final question is why populations do not grow faster in the long term than roughly 0.04%. The answer cannot be physiological (i.e., some reproductive limitation evolved in the Pleistocene, when environment was less productive and much more variable): Many lines of evidence, including the Wyoming-Colorado record, demonstrate populations can grow much faster ($r > 0.4\%$) in the short run. A more plausible hypothesis relates to the ideal free distribution imagined by Fretwell and Lucas (15), who modeled the systematic movement of population from richer to poorer environments. The richer patches, the ones conferring higher individual fitness, are colonized first, and the poorer ones are colonized in order of attraction. Population growth gradually decreases individual fitness in the richest environment until the same fitness can be attained by an individual moving into the next richest environment, which is then colonized, with populations in both environments increasing thereafter in equilibrium until fitness in both patches drops to a point equaled in the third best environment, and so on. This problem affects agriculturalists every bit as much as hunter–gatherers, and it seems possible that population growth rates on the order of 0.03–0.05% might reflect limits imposed by how fast such regional equilibrium can be reached through the reshuffling of population between environments without disrupting essential social ties.

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