Simulating the Global Human Expansion in the Late Pleistocene

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Robert L Bettinger
University of California, Davis

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David A. Young

Lawrence Livermore National Laboratory, Livermore, CA 94550, U.S.A.

Robert L. Bettinger

Department of Anthropology, University of California—Davis, Davis, CA 95616, U.S.A.

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A computer model of human population dynamics is used to study the migration of the first modern humans across the world in the Late Pleistocene. An African origin for modern humans is found to be consistent with archaeological data on the time of arrival of humans in Europe, Australia and the New World. The quantitative model allows for a more precise discussion of human origins and it can be modified and extended as new data and new questions arise.

Keywords: MODERN HUMAN ORIGINS, COMPUTER SIMULATION, OUT OF AFRICA THEORY, MIGRATION.

Introduction

The question of the origin of the modern human population has aroused much controversy in recent years. Molecular-genetic studies have pointed to a recent origin in Africa (Cann, Stoneking & Wilson, 1987), in contrast to some conclusions drawn from fossil human remains, which suggest a more gradual regional evolution throughout the Old World (Wolpoff, 1989). The accumulation of new evidence, both molecular-genetic and archaeological, has not diminished the intensity of the debate (Vigilant *et al.*, 1991; Foley & Lahr, 1992; Stringer, 1992; Cavalli-Sforza, Menozzi & Piazza, 1993; Frayer *et al.*, 1993; Templeton, 1993).

Questions involving population dynamics in space and time are amenable to quantitative analysis, and simple quantitative models can clarify complex processes, thereby allowing more precise debate and discussion. Here we examine the problem of human origins with a space-time computer simulation which mimics the spread of the human population across the world in the late Pleistocene.

Developing the Model

We begin by making an analogy between the dynamics of the early human population and those of animal populations studied by mathematical ecologists (Okubo, 1980; Murray, 1989). A very simple mathematical model for the growth and spatial expansion of the human population is then given by the partial differential equation

$$\frac{\partial P}{\partial t} = RP - DP^2 + \nabla \cdot K \nabla P. \qquad (1)$$

Here ∇ is the vector gradient operator, which contains the space-dependent part of the equation. Appropriate space and time units for a global simulation are kilometres (km) and years (yr). Equation (1) is to be solved for the population density P(x,t), with units of persons km^{-2}, where x is the position variable and t is the time. The fixed parameters which characterize the population are R(yr^{-1}), the population growth rate, D ($person^{-1}\,km^2\,yr^{-1}$), the growth cutoff or carrying capacity term, and K ($km^2\,yr^{-1}$), the diffusion constant. The model population has a simple logistic growth behaviour (first two terms) together with a random-walk spatial motion (last term). This model is based on the assumption that human foragers are dependent on the local ecosystem for survival, which permits a certain maximum population density, given in equation (1) by P_{max}=R/D. The model also assumes that foragers make decisions about moving at the level of the individual or the family, which leads to uncorrelated short-distance movements approximated by the diffusion term in equation (1). The combination of growth and spatial expansion allows equation (1) to have travelling wave solutions (Murray, 1989) in which the population spreads outward from a source point with a constant speed. Such population waves have been observed both in animal and human populations

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(Hengeveld, 1989; Cavalli-Sforza, Menozzi & Piazza, 1993), which makes equation (1) a reasonable first approximation to human population dynamics.

Equation (1) must be solved on an area representing the continents. The surface of the Earth is taken to be a sphere with radius 6371 km, for which the natural polar coordinates are the angles φ (longitude) and θ (latitude). The surface is divided into 7200 zones of size $3° \times 3°$. The continents are built up from rectangular strips in (φ, θ) space, totaling about 2000 zones. Antarctica and Greenland are ignored. Impermeable boundary conditions are imposed for the land-water interface. Equation (1) is written in spherical polar coordinates and is solved numerically on the model area by an explicit-difference method (Gerald & Wheatley, 1985) with a time step of 5 years.

The continental boundaries in the Pleistocene were different from the present boundaries because ice sheets lowered the sea level and exposed the continental shelves. We have not attempted to model the changing boundaries, but we do connect the continents with land bridges to reflect the lower sea levels. We also include the changing ice sheets, since they are effective barriers to migration and settlement, especially in the New World. Ice is modelled by imposing the condition $P=0$ in each zone covered by ice. We include approximate models of the North American and Fennoscandian ice sheets and the more discontinuous Himalayan glaciers. A simple algorithm changes the size of each ice sheet with time based on current geophysical data (Dawson, 1992).

Applying the Model to the Out of Africa Theory

We wish to use equation (1) to simulate and thereby to test the "Out of Africa" theory of human origins. We use archaeological data to fit the unknown coefficients in equation (1). The human population is initiated at a point in Africa and it grows and spreads out across the world in a steady wave. We want the wave to arrive at different points at times consistent with the earliest dated evidence of modern humans at those points. This evidence includes skeletal material or advanced lithic artefacts. Two especially important data are the arrival of modern humans in Southeast Europe by 43 ka bp (1 ka bp=1000 years before present) (Mellars, 1989; Klein, 1992) and the less certain arrival in Australia by 50 ka bp (Roberts, Jones & Smith, 1990). This means that humans departing from Africa probably arrived in Australia before they arrived in geographically closer Europe. To explain this, we postulate that the population growth rate R and mobility K are dependent on environmental conditions. The humans moving out of Africa would be well-adapted to tropical and subtropical conditions and would have a high population growth rate and mobility in these conditions. The population wave could move rapidly across South Asia, Sundaland, New Guinea, and into northern Australia at speeds perhaps as high as $10\,\mathrm{km\,yr^{-1}}$. Once humans began to move into seasonal climate zones, however, they would be less well adapted to the environment and would reproduce and migrate more slowly. Smaller values of R and K are therefore assigned to areas north of latitude 30°, so that the population arrives in Europe and occupies it in accord with archaeological dates. Although the equilibrium population density will surely depend on varying environmental conditions, we have set D to give a maximum density of 0·1 person $\mathrm{km^{-2}}$ everywhere, as a reasonable average value (Hassan, 1981).

Although fossils of anatomically modern humans dating to 100 ka bp are found in Africa and the Levant (Aiello, 1993), evidence of modern humans distant from Africa before 50 ka bp is lacking. It is possible that the capacity for complex culture (Bettinger, 1991), which permitted rapid adaptation to new environments, developed some time after the appearance of modern anatomy, and that the migration did not begin until about 50 ka bp (Clark, 1992; Klein, 1992). We therefore place the population nucleus in East Africa at 50 ka bp and assign it values of $R=0{\cdot}03\,\mathrm{yr^{-1}}$ and $K=1000\,\mathrm{km^2\,yr^{-1}}$. This value of R is probably the highest sustainable growth rate possible for human populations, and it would be characteristic of populations constantly moving into new territory with abundant resources. An example of such high growth and diffusion rates in historic times is seen in the spread of the Neo-Eskimo population across the Arctic (Fagan, 1991). With the given R and K values, the population expanding out of Africa can reach and fill Australia in about 2000 years. Outside of the warm latitudes we assign lower values to R and K. Various combinations of these parameters, such as $R=0{\cdot}001\,\mathrm{yr^{-1}}$, $K=30\,\mathrm{km^2\,yr^{-1}}$ and $R=0{\cdot}01\,\mathrm{yr^{-1}}$, $K=0{\cdot}1\,\mathrm{km^2\,yr^{-1}}$, give nearly identical results. A choice of $R=0{\cdot}01\,\mathrm{yr^{-1}}$, $K=0{\cdot}1\,\mathrm{km^2\,yr^{-1}}$ allows the population to enter Europe at 44 ka bp and fill it by 37 ka bp. Northern Eurasia is filled by about 35 ka bp, and the population wave reaches eastern Beringia and the edge of the North American ice sheet by 20 ka bp. This simulation is shown in Figure 1.

Human cultures over time have successfully adapted to the most varied climatic conditions, so it would be incorrect to maintain the low values of R and K indefinitely for temperate and Arctic environments. Over a time interval of perhaps a few thousand years, the population adapts to local conditions, and then R and K will rise to the values found in the tropics during the initial expansion. Thus we allow the region of potentially optimal growth and mobility to expand slowly until by 20 ka bp it includes the whole Earth.

To model the entry of humans into the New World, we assume that the time of entry was not earlier than 12 ka bp, and that the barrier to entry was the North American ice sheet. When the programmed retreat of the ice sheet opens a passage at 12 ka bp, the Arctic

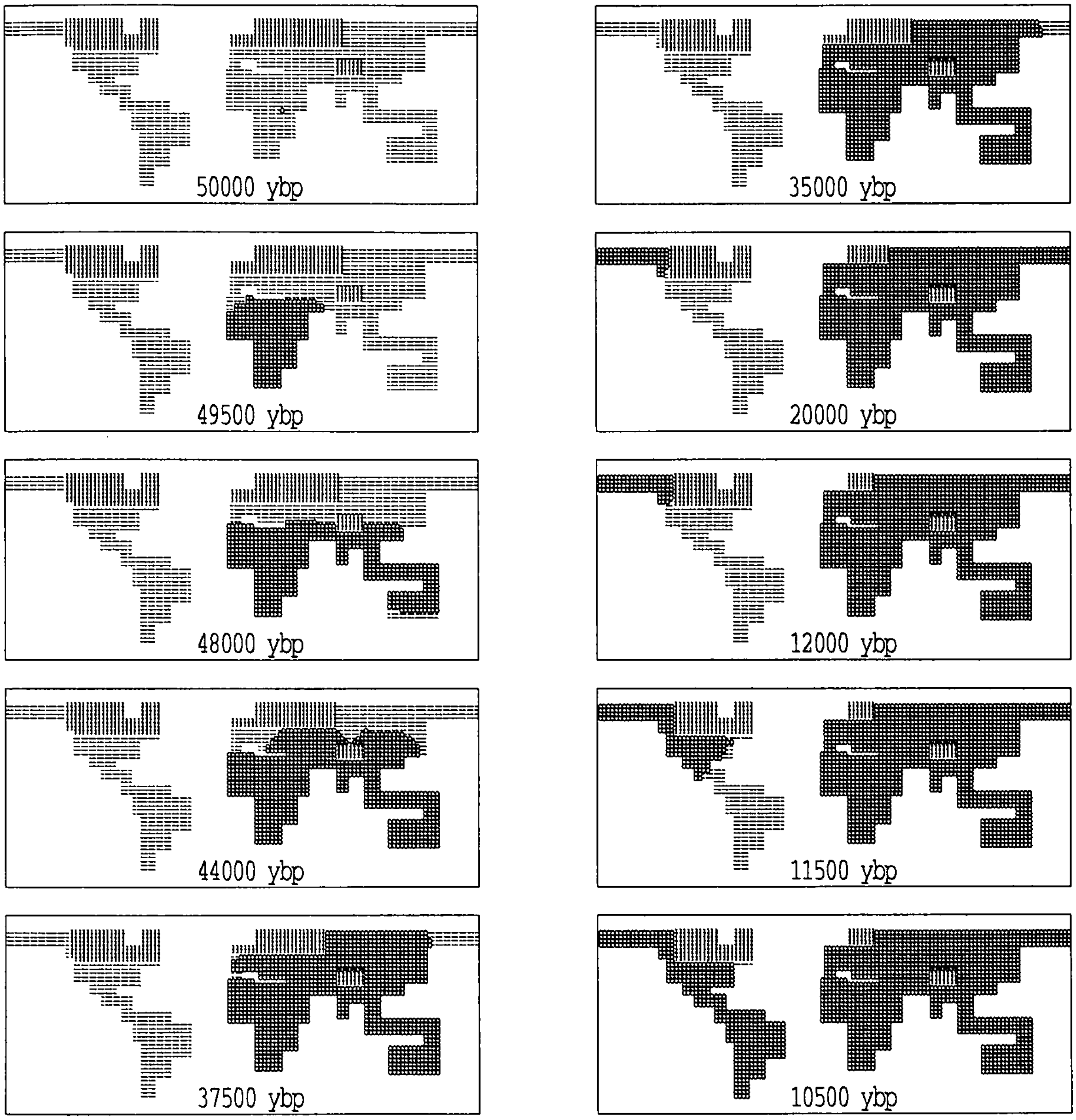

Figure 1. Simulation of the human expansion in the late Pleistocene. The map axes are latitude and longitude. The symbol "—" represents unoccupied zones; "I" represents ice; and "o" represents the human population.

population, having adapted to local conditions over several thousand years, has the high value of growth rate and mobility ($R=0{\cdot}03\ yr^{-1}$, $K=1000\ km^2\ yr^{-1}$), and fills up the New World in about 1500 years. This is in accord with the archaeological record for the New World (Mosimann & Martin, 1975; Dillehay *et al.*, 1992). This is shown in the last two frames of Figure 1.

Results and Discussion

The population wave in Figure 1 is consistent with the time of appearance of Upper Palaeolithic technologies around the world (Wymer, 1982; Roberts, Jones & Smith, 1990; Dillehay *et al.*, 1992; Foley & Lahr, 1992; Hublin, 1992; Klein, 1992; Vasil'ev, 1993). The values we have used for the population growth rate and diffusion constant are consistent with human biology. Although the rapid human occupation of the tropics and of the New World may seem to be anomalous, they are the result of reproductive and migration behaviours well within human capacity. The existence of a steady population wave throughout the simulation is consistent with population pressure as the driving force for the migration, as we should expect. The human expansion is precisely analogous to the biological invasions observed in animal species newly introduced into favourable environments (Hengeveld, 1989). Thus the Out of Africa hypothesis is a possible and plausible model of the global expansion of modern humans.

Could modern humans have exterminated other hominids en route to world occupation? Even slight differences in the mortality rates of competing populations will lead to the extinction of the less competitive one (Zubrow, 1989). This need not involve direct combat or warfare, since it is based on the greater efficiency of one population in gathering food and in reproduction. In our model, the effect of competition between modern and archaic humans would be a reduction in the speed of the population wave as the two populations overlapped. Given the probable advantages that the modern human population had in obtaining food and adjusting to new environments, this reduction in speed would be small. A competition model of this type is worked out in detail for the example of the Numic and Pre-Numic populations of the Great Basin in the 2nd millenium AD (Young & Bettinger, 1992). Thus humans could have replaced Neanderthal or *Homo erectus* populations, as well as other anatomically modern populations which had not made the transition to complex culture, with little effect on the rate of expansion of the human population.

The regional evolution theory is more complex than the Out of Africa theory in terms of numerical modelling. Whereas in the Out of Africa model (Figure 1) the modern human population appears at a point in space and time and then spreads rapidly across the world, in regional evolution modern humans evolve slowly over a very large area of the Old World. Population growth and migration rates are presumably much lower and the population is closer to an equilibrium state. It is probable that such a model could be made to be consistent with the archaeological record, and we therefore do not preclude the regional evolution theory. Obviously further archaeological and genetic research is needed to clarify the problem of human origins.

Human population dynamics in the late Pleistocene were undoubtedly more complex than our very simple model allows, but equation (1) is a useful first approximation. The model makes predictions about the time of arrival of humans in each part of the world, and it can therefore be tested. As new data become available and as more insight into human behaviour in the late Pleistocene is gained, the model can be improved. It is possible that the model could be extended to include descriptions of the evolution and dispersal of languages, technologies, and genes. We believe that computer simulation should be added to the tools available to the archaeologist for decoding the past.

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