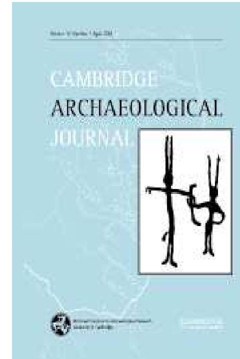

Palaeolithic Populations and Waves of Advance

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Cambridge Archaeological Journal / Volume 14 / Issue 01 / April 2004, pp 53 - 61
DOI: 10.1017/S0959774304000046, Published online: 02 June 2004

Palaeolithic Populations and Waves of Advance

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The wave-of-advance model has been previously applied to Neolithic human range expansions, yielding good agreement to the speeds inferred from archaeological data. Here, we apply it for the first time to Palaeolithic human expansions by using reproduction and mobility parameters appropriate to hunter-gatherers (instead of the corresponding values for preindustrial farmers). The order of magnitude of the predicted speed is in agreement with that implied by the AMS radiocarbon dating of the lateglacial human recolonization of northern Europe (14.2–12.5 kyr BP*). We argue that this makes it implausible for climate change to have limited the speed of the recolonization front. It is pointed out that a similar value for the speed can be tentatively inferred from the archaeological data on the expansion of modern humans into the Levant and Europe (42–36 kyr* BP*).*

From the density distribution of archaeological sites, it is well-established that during the Glacial Maximum (22–16.5 kyr BP) humans abandoned northern Europe in response to the cold, seeking refuge in milder areas (Dolhukhanov 1979; Hahn 1979; Kozlowski & Kozlowski 1979; Bocquet-Appel & Demars 2000a). Recently, Housley and co-workers (1997) performed a detailed archaeological dating for the northward recolonization of northern Europe by hunter-gatherers (Fig. 1). They applied criteria of sound stratigraphical context and unequivocal evidence for human modification of bones and neglected data affected by the use of chemical preservatives for dating, the measurements of questionable chemical fractions, etc. Their careful procedure made it possible for Housley *et al.* (1997) to show that a sequential, well-defined geographical pattern of recolonization is implied by the radiocarbon data. In this article we present a statistical analysis of their data, which allows us to derive the speed of the waves of advancing humans and its error as implied by regression analysis. We also compare this observational range to that predicted by the wave-of-advance model (Ammerman & Cavalli-Sforza 1984; Fort & Méndez 1999) and point out the applicability of the model and parameters discussed to other hunter-gatherer range expansions. The usefulness of such models is that, as we shall see, they make it possible to understand why human range expansions, which are important historical events, take place at the observed speeds and not faster or slower.

The observed speed of recolonization

As in the analysis of the Austronesian population expansion (Fort 2003), we select the oldest site in each of the geographic areas analyzed, in this case from the data by Housley *et al.* (1997). The location and names of the sites are shown in Figure 1. Each number in the map corresponds to the oldest postglacial recolonization site in a circular region with diameter of about 150 km.

In Figure 2, we plot the radiocarbon dates (from Housley *et al.* 1997) for the sites shown in Figure 1 versus their corresponding great-circle distances to the oldest site discovered to date (Kesslerloch, Fig. 1:1). The slope of the regression line (solid line in Fig. 2) is –1.23 ± 0.22 yr/km and is significantly different from zero ($P < 0.001$). The corresponding speed is 0.8 km/yr (0.5–1.1 km/yr with 95 per cent confidence level). The dashed curves around this regression bound the 95 per cent confidence interval.

Cambridge Archaeological Journal 14:1, 53–61
DOI: 10.1017/S0959774304000046 Printed in the United Kingdom

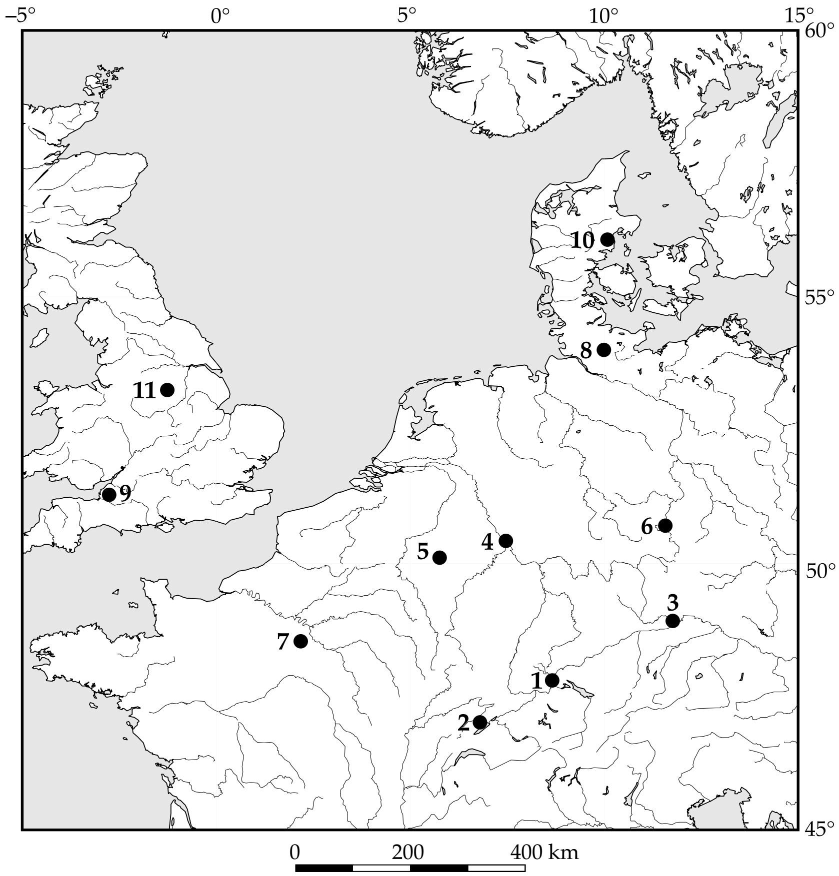

Figure 1. *Map of northern Europe. Each number corresponds to the oldest postglacial recolonization site in a region with diameter of about 150 km. The dates and distances of these sites, from Housley* et al. *(1997), are plotted in Figure 2: 1) Kesslerloch (Schaffhausen, Switzerland); 2) Munroz (Neuchatel, Switzerland); 3) Klausenhöhlen (southern Germany); 4) Andernach (Middle Rhine); 5) Trou des Blaireaux (Belgium); 6) Kniegrotte (eastern Germany); 7) Etiolles (Paris Basin); 8) Poggenwisch (northern Germany); 9) Gough's cave (Mendips, British Isles); 10) Solbjerg (Denmark); 11) Robin Hood's cave (Peak District, British Isles).*

The reason to use the regression of times versus distances is that distance is in principle known exactly, whereas the radiocarbon dates are affected by error (see Sokal & Rohlf 1981). It is true, however, that the actual migration routes may have been influenced by geographical barriers (such as mountains), the distribution of prey species and of gathering resources, etc. It is worth noting, however, that the magnitude of the correlation coefficient is high (r = –0.81). This is why the regression of distances versus times (dotted line in Fig. 2) is rather similar to the former one, and it gives a similar statistical interval for the speed (0.4–0.9 km/yr with 95 per cent confidence level). We may note that the time-versus-distance confidence interval (dashed curves in Fig. 2) includes most of the observational points, which together with the high magnitude of the correlation coefficient supports the applicability of the wave-of-advance model.[1] A low value of the correlation coefficient and the location of many points outside the confidence interval could be interpreted as the result of local perturbations (due, for example, to obstacles and geographic variations in the hunting and gathering resources) that would yield a non-uniform and/or non-isotropic value for the wavefront speed. This is not the case for the data from Housley *et al.* (1997), so that an overall estimation for the wavefront speed makes sense. Thus, in the next section, we will tackle the question of how the observed speed (0.4–1.1 km/yr) may be explained.

For the case of the European Neolithic there are more data, and more reliable, than for the case considered here. This is why the observed speed for the Neolithic (0.8–1.2 km/yr) is less uncertain (compare Fig. 2 here to fig. 4.2 in Ammerman & Cavalli-Sforza 1984). The statistical analysis above, however, shows that for the case of postglacial expansions, the data available at present are enough to make a first step in order to determine the observed speed. It is of course hoped that our analysis can be improved when more and better data become available in the future.

Note that in this section we have determined, by means of a rigorous statistical analysis, what Housley *et al.* (1997) call the pioneer-to-pioneer speed, which corresponds to the leading edge of the wavefront. The pioneer-to-residential speed of Housley *et al.* (1997) cannot be directly compared to the predictions of the wave-of-advance model because it is not the speed of a solution to the reaction-diffusion equation with constant shape (this requirement is necessary to derive Eq. (1) below, see Fort & Méndez 1999 and references therein).

Before closing this section on the observed speed, we would like to mention that Blockley *et al.* (2000) have criticized the approach by Housley *et al.*

(1997) on the following grounds.

i) They claim that a different way to analyze the data (namely, applying 2 sigma instead of 1 sigma errors) gives different values for the earliest dates. This does not, however, change the overall speed: comparing figures 1.a and 1.b in Blockley *et al.* (2000), it is seen that there is the same time interval between the earliest dates for the Upper Rhine and the British Isles, independently of the approach used.

ii) They propose to use a *marine* curve to calibrate the *terrestrial* samples considered by Housley *et al*. (1997). This has been questioned by Housley *et al.* in their response (Blockley *et al*. 2000, 119) and by other authors cited therein. Moreover, it has been argued that until there is consensus for a common calibration system in the Late Glacial, it is better to use uncalibrated dates to avoid confusion (Street & Terberger 1999). This is why we have used uncalibrated dates, as in Housley *et al.* (1997). Even if the calibrations in Blockley *et al.* (2000) were applied, however, the value for the observed speed would be similar to ours. (Note, for example, that the whole time interval in our Fig. 2 is close to that implied by figs. 3 or 4 in Blockley *et al.* 2000.)

iii) Finally, in their figures 5 and 6 Blockley *et al.* (2000) use *all* dates from a given region, rather than the earliest ones in its sites, to estimate the *earliest* date of occupation in the region considered. As Blockley *et al.* (2000) themselves point out, such an approach is counterintuitive. In our opinion, it is also misleading, simply because the longer a site was occupied, the later its computed settlement date would be.

Wave-of-advance model and parameter values

The wave-of-advance model (Ammerman & Cavalli-Sforza 1984) is a mathematical model that leads to a prediction for the speed of advance of a population when it expands its range. As we shall see in more detail below, in order to make such a prediction, one needs some information on how individuals of the biological species concerned (humans in this case) migrate and reproduce.

The wave-of-advance model has been recently refined (Fort & Méndez 1999) by incorporating the implications of two points which we now summarize.

i) Diffusion takes place in two dimensions: this is equivalent to say that individuals do not move only in the south–north or north–south directions (this would correspond to a one-dimensional space) but can also move in the east–west, northeast–southwest or any other direction, i.e. for any angle from 0º to 360º.

ii) There is a delay owing to the mean generation time τ: this is equivalent to say that some time interval passes between the birth of an individual and the time when he or she leaves his/her parents. Such an interval is essentially the mean generation time τ, i.e. the mean age difference between parents and their children.

After taking into account points (i) and (ii) above, the predicted speed is (Fort & Méndez, 1999)

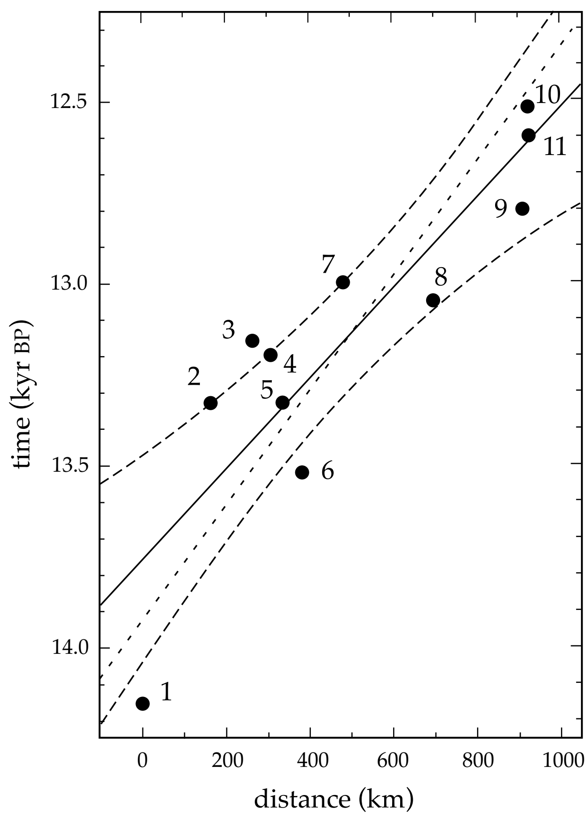

Figure 2. *Determination of the wave-of-advance speed for the lateglacial recolonization of northern Europe. The number at each data point identifies the corresponding site in Figure 1. Distances are measured as great circle routes from the oldest site (Kesslerloch, number 1 in Fig. 1). Radiocarbon dates are from Housley* et al. *(1997). Times are plotted versus distances because of the error in the determination of dates. The continuous straight line is the linear regression fit, and the two dashed curves are 95 per cent confidence-level limits. Distances should not be regarded as without any error, as explained in the text; thus the linear regression of distances versus times is also shown (dotted line). The 95 per cent confidence-level range implied for the speed is 0.4–1.1 km/yr.*

$$v = \frac{\sqrt{a\,m}}{1 + \frac{a\tau}{2}}\ , \qquad (1)$$

where a is the initial growth rate of the population,[2] m is the mobility[3] and τ is the mean generation time (mean age difference between parents and their progeny). Making the diffusion process discontinuous in time introduces a delay, witnessed by the denominator in Eq. (1), which does not appear in the continuous diffusion process modelled by R.A. Fisher and used by Ammerman & Cavalli-Sforza (1984). From Eq. (1), we see that higher values of either a or m will lead to a faster population range expansion, as should be expected intuitively, while the existence of a delay caused by τ will cause a decrease of the rate of advance approximately proportional to τ.

Let us briefly discuss the role of the generation time τ. When a biological species expands its range, some of the individuals migrate to previously empty areas. The generation time is taken as an estimation of the mean time between two subsequent migrations, namely those of the parents and of some of their progeny. This does not imply, however, that individuals migrate only once in their lifetime. Consider for example the case of slash-and-burn agriculturalists. In this case, land is used in a cyclic way so that migrations do happen every few years (Stauder 1971). Once the abandoned areas have recovered their fertility, they are slashed and cultivated again (let us refer to this phenomenon as 'field rotation'). Thus, when a time span of, say, two decades is considered, a productive group occupies a land area that is in fact higher than that they use during, say, a given year. This may also be stated by saying that the true population density (number of people per unit cultivated area) is lower than the value that would be inferred if only the fields being cultivated per year were considered. This is why, in the wave-of-advance model and Eq. (1), the parameters τ and m do not correspond to all 'jumps' but only to one jump per generation (e.g. a son leaving their parents). The effect of other 'jumps' (e.g. field rotations) is included in the population density that appears in the reaction-diffusion equations leading to Eq. (1) (Ammerman & Cavalli-Sforza 1984; Fort & Méndez 1999). But the speed, as given by Eq. (1), is independent of the population density or of its carrying capacity (which is defined as the population density when the population stops growing). Thus, such other 'jumps' do not affect the speed. In contrast, the mean time interval between subsequent migrations τ does appear in Eq. (1) because when the population grows, it is reasonable and consistent with anthropological evidence to consider that some of the sons and daughters will migrate, establish elsewhere and have sons. This is why the value of τ is expected to be similar to the mean generation time.

Eq. (1) implies that a higher value of the mean generation time τ will lead to a slower wave of advance, as should be expected intuitively. In the case of hunter-gatherers, individuals again change their location many times during their lifetime. Similarly to slash-and-burn agriculturalists, this happens in a cyclic way for hunter-gatherers also (Flood 1976; Turnbull 1986). On the other hand, it is reasonable to assume that if the population expands its range, part of the progeny will, after they have grown up, disseminate into previously unpopulated areas. This is why the mean generation time τ and the mean squared displacement m, also per generation, appear in Eq. (1).

It is very important to stress that, as noted explicitly by Bar-Yosef (2002), the wave-of-advance theory gives an overall description that is compatible with more detailed models which take into account the preference of certain environments by the migrating populations (Van Andel & Runnels 1995). Both approaches are alternative descriptions of the same process (Bar-Yosef 2002). The same happens in physics, where transport phenomena can be modelled either by means of macroscopic equations or by the kinetic theory, which corresponds to a more detailed description. Again, the macroscopic equations follow when one averages the microscopic, kinetic ones, so both approaches are consistent (Chapman & Cowling 1990; Jou *et al.* 2001).

Let us return to the problem of human range expansions, which is in fact an example of transport process. The macroscopic, wave-of-advance model makes it possible to derive a quantitative prediction for the overall speed from Eq. (1), whereas the level of detail attained by non-homogeneous models (Van Andel & Runnels 1995) makes them appropriate for the description of the observed clustered distribution of archaeological sites (Ammerman 2002). Both approaches are compatible and one can choose that which is more adequate to deal with the problem at hand. Here we are concerned with the speed of the advance wave. In the previous section we have seen that the available data are consistent with an overall constant and uniform speed (Fig. 2). Therefore we shall apply the wave-of-advance model, which gives a specific, testable prediction for the speed (Eq. (1)). In this context, it is worth mentioning that a time-delayed wave-of-advance model has been very recently applied successfully to explain the range expansion of a completely different biological population, namely T7 viruses in a medium composed of agar and *E. Coli* cells. In this case, the speeds predicted under various conditions are in agreement with those observed in the laboratory experiments (Fort & Méndez 2002). That application, together with the satisfactory predictions of the wave-of-advance model for Neolithic populations (Fort & Méndez 1999; Fort 2003), makes it a reasonable candidate to describe the range expansions of hunter-gatherers.

In order to avoid any possible confusion, it is worth stressing that all wave-of-advance models so far applied assume that new generations of individuals wander without any preferred direction. In the case of Neolithic populations (Ammerman & Cavalli-Sforza 1984; Fort & Méndez 1999; Fort 2003), people wander in search of new lands to farm. In the case of Palaeolithic populations (present article), they wander in search of food resources to hunt and/or gather.

In order to apply the time-delayed wave-of-advance model, we need numerical values for the parameters m, a and τ so that we can compute the speed predicted by Eq. (1). Previous studies on human expansions dealt with waves of advance of Neolithic communities, thus the theoretical predictions made use of parameters derived from anthropological observations of preindustrial farmers. This approach was applied to the Neolithic transition in Europe (Ammerman & Cavalli-Sforza 1984; Fort & Méndez 1999) and Oceania (Fort 2003). Here we are dealing with hunter-gatherers instead of farmers. Therefore the necessary parameter values (m, a and τ) have to be derived from the ethnography of hunter-gatherers. Nevertheless, it will be interesting to discuss briefly their differences from the corresponding data for preindustrial farmers.

Values of the mobility per generation m used in models of the Neolithic transition in Europe were estimated from observed distributions of distances between birthplace and place of residence of the Gilishi and Shiri communities of the Majangir, who are slash-and-burn agriculturalists in Ethiopia (Stauder 1971). The range of values for m implied by those data is 1100–2200 km^2 per generation (Ammerman & Cavalli-Sforza 1984, 155). For hunter-gatherers, m can again be estimated from the distributions of distances between birthplace and place of residence. For Aka and Bofi-Aka African pygmies, such distributions were recorded (Hewlett *et al.* 1986) and they yield the range 1400–3900 km^2/generation for m. We note that there is a wide uncertainty range in both cases, but the mean mobility of hunter-gatherers is higher. This may also be observed from the distributions of distances between the birthplaces of spouses (Ammerman & Cavalli-Sforza 1984, 79; Hewlett *et al.* 1986), although in general this does not correspond directly to the displacement per individual and generation (Hewlett *et al.* 1986).

The initial growth rate of farmers is known rather precisely. Birdsell (1957) collected data for human populations who settled in empty space at different times and places (Bass Strait Islands and the Pitcairn island). When the population size is plotted against the generations of elapsed time, there is excellent agreement between both sets of data, yielding the range for a 0.73–0.86 gen^{-1}. If a mean generation time of 25 yr is used (Ammerman & Cavalli-Sforza 1984, 156) this yields the range 0.029–0.035 yr^{-1} for a. It is very interesting that for the U.S. colonization in the nineteenth century, Lotka (1956) obtained essentially this same value for a. In fact, for the U.S. colonization there are historical census data for many different regions (http://fisher.lib.virginia.edu/census/) and they give very similar results (D. Campos pers. comm.). Thus the range of a is known rather precisely for agricultural populations.

It may be useful to remember that in the wave-of-advance theory, the growth rate a refers to the initial growth at the beginning of the logistic curve,[1] which is the fastest, and applies only at the front of the wave of advance, because there the population density is very small.

The few modern hunter-gatherers still in existence are rather restricted in their growth by extreme limitations in the environment they occupy, and have a rate of growth very close to zero or often negative and are, moreover, mostly in transition to other economies. As far as we know, similar data series to those quoted above are not available for hunter-gatherers, but the differences in fertility between preindustrial farmers and hunter-gatherers are well-known. They may be used to estimate the value of a for hunter-gatherers by means of the formula[4]

$$a = \ln \frac{f(1-M)}{2}, \qquad (2)$$

where a is the initial growth rate per generation,[3] f is the fertility rate (mean number of children per woman at the end of her reproductive life) and $M < 1$ is the subadult mortality rate, which is essentially the same for preindustrial populations, independently of whether they are farmers or hunter-gatherers (Sellen

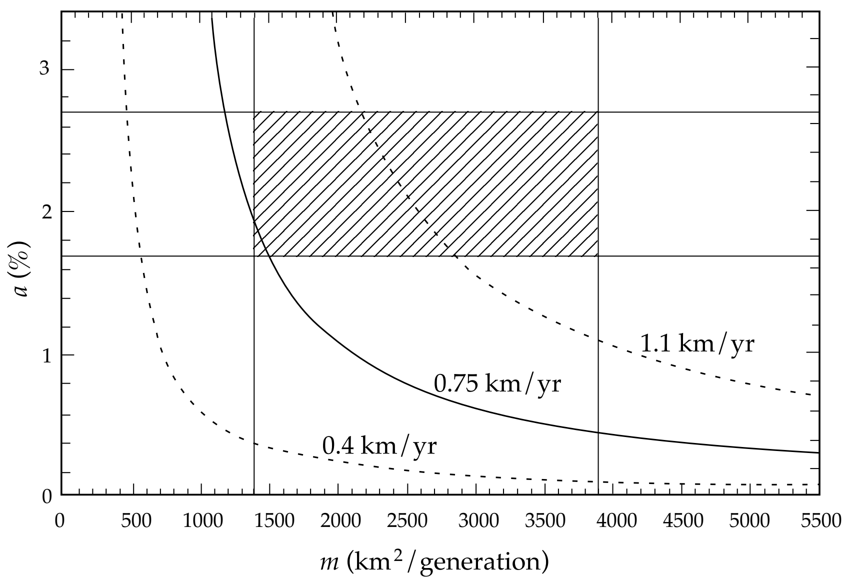

Figure 3. *Comparison between the predictions of the wave-of-advance model and observations. The hatched rectangle corresponds to the allowed ranges of values for the parameters a and m (Table 1). The curves give the values of* a *and* m *that predict a value for the speed of 0.4, 0.75 and 1.1 km/yr. It is seen that the observed speed range (0.4–1.1 km/yr, from Fig. 2) is consistent with the predictions of the model.*

2000, 52 & table 2). Thus, if the fertilities of hunter-gatherers and farmers (f_{HG} and f_F, respectively) are known, their initial growth rates a_{HG} and a_F (measured in gen^{-1}) can be related through[5]

$$a_{HG} = a_F + \frac{\ln f_{HG}}{\ln f_F} \, . \qquad (3)$$

The fertilities of many preindustrial populations have been measured, yielding consistent results of f_{HG} = 5.3 and f_F = 6.5 (Sellen & Mace 1997). Then Eq. (3) and the range above for a_F yield the range for a_{HG} 0.52–0.66 gen^{-1}. In order to convert this into year units, it must be taken into account that hunter-gatherers have a mean interval between successive births that is about two years higher than the corresponding one for preindustrial farmers (Ammerman & Cavalli-Sforza 1984). A generation time of 27 years is also suggested by Weiss (1973). Thus we use a mean generation time of 27 years for hunter-gatherers. The range above for a_{HG} is 0.019–0.025 yr–^{1}, or 1.9–2.5%. We will allow for the wider range 0.017–0.027 yr^{-1}, or 1.7–2.7%, so as to allow for possible uncertainties in the determination of the fertility rates and generation times used in the estimation of a_{HG} above.

Discussion

Table 1 compares the relevant parameters for farmers and hunter-gatherers, which have been obtained in the previous section. As noted above, mobility is higher for hunter-gatherers. From Eq. (1) it is clear that this tends to yield higher speeds. The growth rate and mean generation time, however, are lower for hunter-gatherers, which has the opposite effect. Indeed, from the *mean* values in Table 1 and Eq. (1) one obtains v = 1.0 km/yr for farmers and 1.1 km/yr for hunter-gatherers, which are similar speeds as far as the order of magnitude is concerned.

Changing the value of the mean generation time leads to much the same result for the speed (Fort & Méndez 1999). In Figure 3 we present the predictions of Eq. (1) for the ranges of a and m for hunter-gatherers estimated above (hatched rectangle in Fig. 3). It is seen that Eq. (1) predicts a speed v between 0.7 and 1.4 km/yr. Since the speed determined from the archaeological data is 0.4–1.1 km/yr (Fig. 2), we see that the wave-of-advance model is consistent with the observed speed. It must be noted, however, that agreement holds only for the lower range of the mean-squared displacement per generation ($m < 3000$ km^2/gen). This shows that (i) the wave-of-advance model is consistent with available evidence; (ii) more data on the mobility of hunter-gatherers would be useful to narrow further the predictions of the model. Also, we stress again that, if the number of archaeological sites is increased by future discoveries, it will be possible to determine the observed speed more precisely (compare Fig. 2 here to fig. 4.2 in Ammerman & Cavalli-Sforza 1984).

It may be argued that if the return to mild conditions after the glaciation had been sufficiently slow, it could in principle have slowed down the hunter-gatherers' recolonization. This seems unlikely, however, if we take into account that, according to the evidence available at present:

i) the ice sheets were well to the north of the area examined by 13,000 yr BP (Housley *et al.* 1997, fig. 1);

Table 1. *Comparison between typical values for the diffusion* (m)*, delay* (τ) *and growth* (a) *parameters for preindustrial farmers and hunter-gatherers. The most difficult parameter to estimate is the mobility* m*. The value of the mean generation time* τ *has little effect on the speed predicted by Eq. (1) (Fort & Méndez 1999). Note that hunter-gatherers are more mobile but have a smaller initial growth rate because their fertility is lower. The way estimations have been performed is explained in the text.*

	preindustrial farmers	**hunter-gatherers**
m (km^2 /generation)	1100–2200	1400–3900
τ (years)	**25**	**27**
a (years^{-1})	0.029–0.035	0.017–0.027

ii) archaeological remains dated 40,000 yr BP have been recently found in the Russian Arctic (Pavlov *et al*. 2001); and
iii) temperature and pollen diagrams indicate that the climate after 15,000 yr BP was significantly milder than 40,000 yr BP (Gowlett 2001, fig. 1).

Although the timing of ice cover melt as a function of location is not known precisely (Crowley & North 1991; Gowlett 2001), these arguments make it implausible that it could have lowered the speed of the hunter-gatherers' population front. The argument may be reversed by saying that the speed of the observed recolonization (Fig. 2) can be regarded as evidence for a return to mild conditions after the glaciation at a speed of at least 0.4 km/yr. If the environmental conditions that previously forced humans to abandon northern Europe had improved at a slower rate, it would not have been possible for them to recolonize the north at this speed. The order-of-magnitude agreement with the model predictions (Fig. 3), which does not incorporate climate change but assumes an uniform habitat, is satisfactory and consistent with this view.

It is well-known from palaeoclimatology that the European climate deteriorated again once the hunter-gatherer recolonization here discussed was completed. This new cooling happened during the so-called Younger Dryas (~10,000–11,000 yr BP). The North Atlantic polar front came back towards the south, sweeping again all of northern Europe (Crowley & North 1991, fig. 3.16). Did this event cause a new depopulation of northern Europe and, if so, what was the speed of the new recolonization front? At present we do not know the answers, but archaeological data could be useful to solve this problem in the future. Moreover, according to the environmental data available, warming periods (~13,000 yr BP for the lateglacial, ~10,000 yr BP for the Yonger Dryas) were very rapid, whereas the cooling (~13,000–10,000 yr BP) was much slower (see e.g. Crowley & North 1991, fig. 3.13). This may indicate that the speed of depopulation fronts was in fact limited by the climatic rate of change, while recolonization ones were not, as discussed above for the lateglacial. It will be possible to test such a general framework against empirical evidence only when numerous and sufficiently accurate archaeological data for the processes mentioned become available.

Finally, it is worth mentioning that there are some data for a different hunter-gatherer range expansion, namely that into the Levant and Europe by modern humans (42–36 kyr BP). It is interesting that in this case, the few data available (see e.g. Bar-Yosef & Pilbeam 2000; Stringer *et al.* 2000; Gibbons 2001, 1725) imply that the incoming human wavefront travelled a distance of some 3000 km during 6000 yr, which would correspond to a speed of about 0.5 km/yr. This should not be regarded at all as a precise value for the speed, however, because the data are scarce and rather uncertain: the oldest sites have a dating error of ~2000 yr (Bar-Yosef *et al.* 1996), which could lead to a change in the speed of a factor of two. In comparison, for the late glacial wave of advance we have discussed, the typical dating error is ~150 yr (Housley *et al.* 1997). This, and the scarcity of dated sites, is why a detailed statistical analysis does not seem appropriate at present in the case of the original wave of advance of modern humans. It is very interesting, however, that:
i) additional data by Bocquet-Appel & Demars (2000b) (especially Figs. 8.d & 8.e) indicate a speed of about 0.8 km/yr for the expansion of modern humans across Europe, which is very similar to the estimation of 0.5 km/yr above;
ii) this *order of magnitude* for the speed is the same as that observed for the lateglacial recolonization (0.4–1.1 km/yr, from Fig. 2) and with that predicted by the wave-of-advance model (Fig. 3).

Thus, we have presented a methodology that can be useful also in the future, when the number and precision of the archaeological data allow for more precise determinations of the speeds for other hunter-gatherer waves of advance.

Acknowledgements

We thank D. Campos for information on webpages with historical census data on the U.S. colonization and their implied values for *a.* Suggestions by M.T. de Pouplana on a previous version are also acknowledged. Computing equipment was funded in part by the CICYT of the Ministry of Science and Technology under grants BFM2000-0351 (JF) and REN2000-1621 CLI (JF and TP).

Notes

1. The magnitude $|r|$ of the correlation coefficient r always satisfies that $0 \le |r| \le 1$. If this magnitude has a high value, as in our case, it means that the data points are close to the fitted straight line (Fig. 2), i.e. that the data support a linear relationship between space (moved by the wave of advance) and time. A linear relationship between space and time is equivalent to a constant speed, which is a prediction of the wave-of-advance model.
2. Biological populations, including human ones, are observed to grow exponentially in number if they consist of sufficiently few individuals initially. The exponent is proportional to the time elapsed, and the proportionality constant is called the initial growth rate (we denote it with the symbol a). Because food and space available are not infinite, however, an exponential increase cannot be maintained indefinitely, and at some point the population number begins to increase more slowly, until it eventually stops growing. The population number is thereafter a constant. Thus the typical population number–versus time curve has an 'S' shape. The mathematically-simplest such curve is called the logistic curve. For more information, see e.g. Lotka (1956).
3. The mobility m is the mean-squared displacement per generation. For example, if an individual has moved 1.5 km away from his or her birthplace and a second individual has moved 2 km away from his or her birthplace, then their mean (or average) square displacement is $m = (1.5^2 + 2^2)/2$. In practice one averages over many, rather than only two, individuals in order to estimate m. The reason why distances are squared is that otherwise the derivation of Eq. (1) (Fort & Méndez 1999) would not be valid.
4. This is a well-known formula (Hassan 1981, 139). A simple derivation is possible: as explained in note 1, an initially low population density n will grow exponentially, as $n = n_{t=0}e^{at}$. From this, we can evaluate n at $t = 1$ generation, which yields

$$a = \ln \frac{n_{t=1\text{ generation}}}{n_{t=0}}.$$

   The fraction inside the logarithm is obviously the fecundity (number of children per woman) divided by two (because n includes men in addition to women) and corrected by the mortality. In this way we obtain Eq. (2).
5. Eq. (3) follows from writing Eq. (2) for farmers:

$$a_F = \ln \frac{f_F(1-M)}{2},$$

   and for hunter-gatherers:

$$a_{HG} = \ln \frac{f_{HG}(1-M)}{2},$$

   and subtracting both equations.

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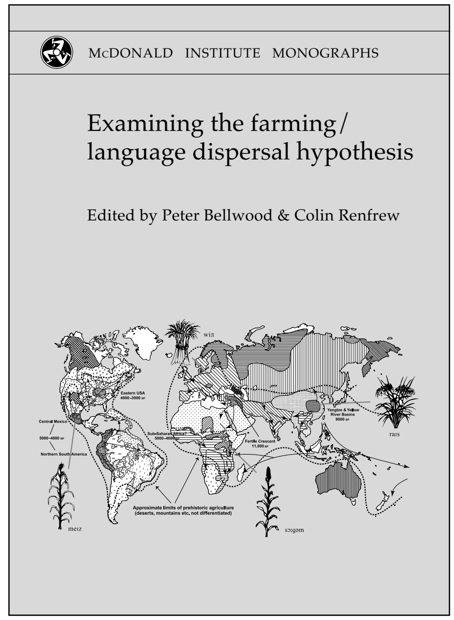
Title: *Examining the farming/language dispersal hypothesis*
Editors: Peter Bellwood and Colin Renfrew
Series: McDonald Institute Monographs
Classifications: Archaeology; Historical Linguistics; Genetics; Farming origins
Binding: Cloth
Size: 286 × 220 mm
Pages: xiv+505 pp.; 80 illustrations, 25 tables
ISBN: 1-902937-20-1 hardback
ISSN: 1363-1349
Price: £50; US$85
Publication date: July 17, 2003
Distributor: Oxbow Books, Park End Place, Oxford, OX1 1HN, UK. Tel: (01865) 241249; www.oxbowbooks.com - *or* - David Brown Book Co., P.O. Box 511, Oakville, CT 06779, USA. Tel: 860-945-9329; Fax 860-945-9468



Linguistic diversity is one of the most puzzling and challenging features of humankind. Why are there some six thousand different languages spoken in the world today? Why are some, like Chinese or English, spoken by millions over vast territories, while others are restricted to just a few thousand speakers in a limited area? The farming/language dispersal hypothesis makes the radical and controversial proposal that the present-day distributions of many of the world's languages and language families can be traced back to the early developments and dispersals of farming from the several nuclear areas where animal and plant domestication emerged. For instance, the Indo-European and Austronesian language families may owe their current vast distributions to the spread of food plants and of farmers (speaking the relevant proto-languages) following the Neolithic revolutions which took place in the Near East and in Eastern Asia respectively, thousands of years ago.

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