

Mathematical models of the Neolithic transition: a review for non-mathematicians

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Abstract

This paper reviews mathematical models of the Neolithic transition and their comparison to archaeological observations. We also discuss regional variations of the spread rate, and outline possible non-homogeneous extensions of the existing mathematical models.

1. Introduction

This paper surveys the main existing mathematical models of the Neolithic transition. They are presented in their historical context, in a self-contained way, and using as few mathematics as possible. Still, we reproduce all necessary formulae to reach the results reviewed.

Section 2 presents the classical model by Ammerman and Cavalli-Sforza. Some later refinements of their model are surveyed in sections 3 to 6. We also compare the speed predicted by each model to that implied by the archaeological data. Section 7 contains a new derivation of a recent model. Regional variability is discussed in sections 8 and 9 (using archaeological data and mathematical models, respectively). Finally, section 10 is devoted to concluding remarks.

2. The model by Ammerman and Cavalli-Sforza

While working at Fisher's laboratory in Cambridge from 1949 until 1951, Cavalli-Sforza learnt [1] about Fisher's model. It was initially conceived to describe the spread of advantageous genes [2], and later applied to biological invasions [3]. Cavalli-Sforza noted that, if the Neolithic transition was not a process of cultural imitation but mainly due to the dispersal of populations, then: (i) Fisher's equation could hold, and (ii) the values of its parameters could be estimated from anthropological data. This was the first mathematical model of the Neolithic transition. Indeed, according to Fisher's model the population front speed (in kilometers per year) is predicted as [2,3]

$$c_{\text{predicted}} = 2\sqrt{aD}, \quad (1)$$

where a is called the initial growth rate of the population number and D is the population diffusion coefficient.

The faster a population reproduces, the higher its value of a will be, and according to equation (1) the invasion front will spread faster. Similarly, the further away individuals disperse from their parents, the higher the value of D will be and, again, equation (1) predicts a faster invasion.

Ammerman and Cavalli-Sforza [4] gathered the archaeological data available and used them to estimate an observed speed of

$$c_{\text{observed}} = 1.0 \pm 0.2 \text{ km/yr.} \quad (2)$$

They also estimated the diffusion coefficient as [6]

$$D \approx \frac{\langle \Delta^2 \rangle}{T}, \quad (3)$$

where T is the generation time. Finally, Ammerman and Cavalli-Sforza [6] also found anthropological observations in the literature for human reproduction, mobility and the generation time T . Those anthropological observations yield the characteristic values

$$a = 0.032 \text{ yr}^{-1}, \quad (4)$$

$$\langle \Delta^2 \rangle = 1544 \text{ km}^2, \quad (5)$$

$$T = 25 \text{ yr.} \quad (6)$$

Using these values into equations (3) and (1) yields

$$c_{\text{predicted}} = 2.8 \text{ km/yr.} \quad (7)$$

The prediction (7) is much faster than the speed (2) observed from the archaeological record.

The characteristic mobility value (5) was obtained from *individual* mobility data per generation for pre-industrial agriculturalists [5]. Some *mating* data (distances between birthplaces between husbands and wives) yield much lower values of $\langle \Delta^2 \rangle$, and thus of the predicted speed (1) [6]. However, mating data seem inappropriate

because derivations of Fisher's model [7,8] show that $\langle \Delta^2 \rangle$ corresponds to distances Δ moved *per individual* during the generation time T (i.e., distances moved by individuals from their birthplace until the place where they have children).

This theoretical model, proposed by Ammerman and Cavalli-Sforza in 1984, was the first mathematical computation of the predicted speed of the Neolithic transition [6].

3. Fisher's model in two-dimensional space

Equation (3) gives an order-of-magnitude estimation of the diffusion coefficient D . However, its precise value depends on the number of dimensions, as follows.

(i) For a one-dimensional space (e.g., a population of birds dispersing along a coast) [7],

$$D = \frac{\langle \Delta^2 \rangle}{2T}, \quad (8)$$

(ii) For a two-dimensional space (e.g., a population of humans invading Europe) [8],

$$D = \frac{\langle \Delta^2 \rangle}{4T}, \quad (9)$$

(iii) For a three-dimensional space (e.g. a fish population in an ocean),

$$D = \frac{\langle \Delta^2 \rangle}{6T}, \quad (10)$$

As it might be expected intuitively, D and therefore the invasion speed (1) are lower the higher the number of available dimensions into which the population can disperse.

Using the observed values (5)-(6) into the two-dimensional formula (9) yields

$$D = 386 \frac{\text{km}^2}{\text{gen}} = 15.44 \frac{\text{km}^2}{\text{yr}}, \quad (11)$$

which used into equation (1) (with the same values of a and T as above) leads to

$$c_{\text{predicted}} = 1.4 \text{ km/yr.} \quad (12)$$

This is a more accurate estimation than (7). However, it is still outside the observed range from the archaeological observations quoted in equation (2), namely 0.8-1.2 km/yr [4].

4. Time-delayed model

A more refined approach [8] noted that Fisher's speed (1) does not take into account the fact that newborn children spend some time T with their parents until they become adults and can migrate. If this effect is taken into account, the predicted speed is

$$c_{\text{predicted } T} = 2 \frac{\sqrt{aD}}{1 + \frac{aT}{2}}, \quad (13)$$

instead of Fisher's speed (1). Note that if the effect of the dispersive delay is neglected ($T = 0$), equation (13) reduces to Fisher's speed (1), as it should.

Using the same parameter values as above, the more refined prediction (13) yields a speed of

$$c_{\text{predicted } T} = 1.0 \text{ km/yr,} \quad (14)$$

which is consistent with the observed range (0.8-1.2 km/yr).

5. Mathematical models versus archaeological observations

Figure 1 shows the distances to Jericho (the presumed center of the Neolithic population dispersal) versus the oldest date of archaeological sites, according to the data used by Ammerman and Cavalli-Sforza [4,6]. The full line is their fit to the data. The distance-versus-dates and dates-versus-distances regressions (not shown) yield the observed speed quoted in equation (2), namely 1.0 ± 0.2 km/yr (95% confidence interval) [8]. Each of the three other lines in figure 1 gives the best fit using the speed predicted by each of the three models above, namely (7), (12) and (14). The value of χ^2 is the error of the considered model, relative to the data (i.e., the sum of the squared distances). Clearly the prediction of equation (13) gives a lower error than those from the non-delayed models (7) and (12).

A sensitivity analysis using the observed error ranges for the values of the parameters (4)-(6) was also performed, reinforcing the conclusion that the non-delayed models (sections 3 and 4) give too fast speeds as compared to the archaeological record [8].

As mentioned above, the distance-versus-dates and dates-versus-distances regressions of the 53 sites in figure 1 lead to an observed speed range of 1.0 ± 0.2 km/yr. However, that dataset is now over thirty-five years old [4]. Therefore, it is very important to know if archaeological data available today yield a similar speed range or not. Gkiasta et al [17] performed such an analysis with 510 sites and obtained a speed of 1.3 km/yr. However, they did not compute an error range for this speed. And they assumed that Jericho was the origin of the dispersal. However, a different presumed origin will yield a different speed. As stressed by Ammerman and Cavalli-Sforza, the most probable origin should be that which yields a higher correlation coefficient. Such an analysis has been recently performed for 735 sites, and the speed range (using again great-circle distances) is 0.7-1.1 km/yr. Again, this range was computed from combining the distance-versus time and the time-versus-distance regressions (figure 2.a). This speed range (0.7-1.1 km/yr) can be viewed as a comforting result, because it is compatible with that obtained by Ammerman and Cavalli-Sforza 35 years earlier (0.8-1.2 km/yr). There is no inconsistency and, therefore, this seems to be a sound line of research.

6. Cohabitation models

Let $p(x, y, t)$ stand for the population density (i.e., the number of individuals per unit area centered at the space point (x, y) at time t). Fisher's speed (1), as well as its time-delayed generalization (13), can be derived by assuming that, for low values of the population density $p(x, y, t)$,

$$p(x, y, t+T) = R_0 p(x, y, t) + \sum \Pi(x', y' \rightarrow x, y) p(x', y', t) \quad (15)$$

where the net reproductive rate R_0 depends on the initial growth rate a (appearing in equation (1)) as $R_0 = e^{aT}$ [9]. In the last term, $\Pi(x', y' \rightarrow x, y)$ is the probability than an individual moves from (x', y') to (x, y) . The sum Σ indicates that we take into account all possible origins (x', y') .

Recently it has been argued that a more realistic model should be the following [9]

$$p(x, y, t+T) = R_0 \sum \Pi(x', y' \rightarrow x, y) p(x', y', t). \quad (16)$$

Similar models are widely used in Ecology [10-12]. The difference is that model (15) considers that children appear at the same location as the parents (first term in equation

(15)), and parents migrate away from their children (last term). This is not realistic for human populations. In contrast, equation (16) considers that children grow up with their parents at their final location. Thus equation (16) is a cohabitation model, whereas (15) is not. The same conceptual limitation applies to Fisher's model (1) and its time-delayed generalization (13), because they are both special cases of the model (15). The differences between the cohabitation model (16) and the model (13) are as large as 30% [9]. However, the speed range predicted by (16) is still consistent with the observed range [9], namely 0.7-1.1 km/yr (from figure 2.a).

7. Dispersive-variability models

In this section we present a new derivation of the cohabitation model, reviewed in the previous subsection. This derivation is motivated by work by other authors showing the importance of taking the age-structure of populations into account in mathematical models [13], as well as by some recent dispersive-variability models [15,16].

Any human population can be regarded as composed by three sub-populations, with different behaviors: juveniles (e.g., individuals $< \tau$ years old, where τ is the age at first reproduction), reproducing adults (e.g., aged $\geq \tau$ years old and reproducing), and non-reproducing adults (because of age, sterility, or other reasons). Let $p_J(x, y, t)$, $p_A(x, y, t)$ and $p_{AN}(x, y, t)$ stand for the corresponding numbers of individuals per unit area centered at position (x, y) at time t .

Obviously, the number of juveniles appearing per generation should be related to the number of reproducing adults in the preceding generation $p_A(x, y, t)$, not to the total number of individuals, i.e.

$$p(x, y, t) = p_A(x, y, t) + p_J(x, y, t) + p_{AN}(x, y, t).$$

How can we write down such a relationship mathematically? If we consider (as a useful approximation) a simple, time-averaged model in which all individuals begin to reproduce at once, we can simply write

$$p_J(x', y', t + T_1) = f p_A(x', y', t). \quad (17)$$

where f is the population fecundity, and T_1 is the mean age difference between the first and the last child.

In agreement with anthropological observations [5], let juveniles to migrate away from their parents after some mean time T_2 . Then,

$$p_A(x, y, t + T_1 + T_2) = s \sum \Pi(x', y' \rightarrow x, y) p_J(x', y', t + T_1), \quad (18)$$

where s is the fraction of juveniles who will become reproducing adults, and $\Pi(x', y' \rightarrow x, y)$ is again the jump probability from (x', y') to (x, y) .

Of course, more complicated models can be considered. But this simple model is more detailed than those in the previous sections, because here we take into account that the reproductive and dispersive behavior may depend on age (albeit in the simplest possible way). How does the front speed change when considering this more detailed description? Interestingly, it does not change at all! Indeed, making use of the first equation into the right-hand side of the second one, and defining $T = T_1 + T_2$, we come to

$$p_A(x, y, t + T) = R_0 \sum \Pi(x', y' \rightarrow x, y) p_A(x', y', t), \quad (19)$$

where $R_0 = s f$. So we obtain again the cohabitation model, given by equation (16). The only difference is that here the reproducing adult subpopulation $p_A(x, y, t)$ appears,

instead of the total population $p(x, y, t)$. But the important point is that the speed of invasion front solutions is the same as for the cohabitation model in the former section. This gives further support to the cohabitation model. It also shows that it is always possible to build more complicated mathematical models, but in some cases this does not lead to any new prediction that can be compared to the archeological data. So it does not seem worth to complicate the model in the previous section further (in this direction). Instead, a good guide is given by a quote by Albert Einstein: "*Mathematical models should be kept as simple as possible -but not simpler*".

8. Regional variability: archaeological observations

According to the mathematical models reviewed above, the speed of the Neolithic front is a constant. This predicts that all data points in figure 1 should fall on a straight line. Clearly this is not the case. Some possible reasons are the following:

(i) Errors in the radiocarbon dates and/or the computed distances. The latter can be due to the existence of several independent spatial origins of agriculture (e.g., an origin for wheat, another one for barley, etc.), to the unavailability of some regions for human settlement (seas and high mountains), etc.

(ii) Regional variability in the spread rate. This should show up as most data points (for the region considered) falling either to the right or to the left of the regression (full line in figure 1). If the spread slows down in a region, sites will be younger than average, and fall on the right of the regression (more recent dates). Conversely, if the spread accelerates in a region, its sites will be older than average and fall to the left of the regression. For example, Ammerman and Cavalli-Sforza [4] mentioned a definite slowing down of the spread in Scandinavia. Does their observation hold up for the archaeological data available today? To answer this question, in figure 2.b we repeat the same regressions as Fig. 2.a, but only the 38 sites from Denmark (from the 735 sites in Fig. 2.a). Clearly, most data points in figure 2.b lie to the right of the regressions. Therefore, the new data confirm that the spread was indeed slowed down in Denmark. No mathematical model has so far explained this observation -less still the values of its delay time in years.

In the next section, we will discuss how regional variability could be included in mathematical models. But before doing so, let us mention that besides the slowing down of the spread in Northern Europe, there are additional archaeological observations of regional variation that deserve attention, e.g. the delay into the Alpine area [6,17], the accelerated spread of the Bandkeramik in central Europe [4], and the extremely fast rate along the Western Mediterranean [4,18] (interestingly, the latter is similar in speed to the Neolithic expansion in Oceania [19]).

9. Regional variability: mathematical models

Regional variability can be due to many possible reasons, such as:

(i) Geographic or climatic barriers. They are a possible explanation for what appears as a 1,000-year stop of the Neolithic spread into Southern Scandinavia, due to a slow shift from hunter-gatherer into farming economics, possibly because of local difficulties in the practice of agriculture [20]. Such a stop does not appear of purely cultural origin, but ultimately due to geographic factors.

(ii) Cultural effects. Regions of fast acculturation by hunter-gatherers could in principle show a faster spread (and reduce the coexistence time between hunter-gatherers and farmers, which can be estimated from archaeological data).

Mathematically, only recently several-population models have described cultural diffusion effects [21,22,23]. This is a wide topic that deserves further work.

(iii) Non-homogeneous values of demographic parameters. From a purely mathematical perspective, this may correspond either to human dispersal parameters (diffusion coefficient D , dispersal probability distribution $\Pi(x',y' \rightarrow x,y)$, time interval between subsequent migrations T) or reproductive ones (values of a and R_0). However, we are not aware of any anthropological data backing such suggestions.

(iv) Anisotropic dispersal effects. When the invading population front enters a region unsuitable for agriculture, humans may have a higher tendency to migrate backwards than forwards. There is some anthropological support for this suggestion, because migration data for the human colonization of Northern America in the XIX century are indeed anisotropic. Mathematical models including such effects have been recently proposed [24,25].

10. Conclusions

We have surveyed the main mathematical models of the Neolithic transition, as well as their comparison to archaeological observations.

Some additional models, e.g. models with several values of the generation time [26], have not been reviewed in this paper (mainly because they yield similar results for the predicted spread rate to the models here surveyed).

As reviewed in section 8, archaeological data show that regional variations in the spread rate are important. This is an interesting point that deserves further efforts using mathematical models, such as those summarized in section 9.

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References

- [1] L. L. Cavalli-Sforza, Recollections of Whittingehame Lodge, *Theor. Popul. Biol.* 38, 301-305 (1990).
- [2] R. A. Fisher, The wave of advance of advantageous genes, *Annals of Eugenics* 7, 355-369 (1937).
- [3] J. G. Skellman, Random dispersal in theoretical populations, *Biometrika* 38, 196-218 (1951).
- [4] A. J. Ammerman and L. L. Cavalli-Sforza, Measuring the rate of spread of early farming in Europe, *Man* 6, 674-688 (1971).
- [5] J. Stauder, *The Majangir. Ecology and society of a southwest Ethiopian people* (Cambridge University Press, Cambridge, 1971).
- [6] A. J. Ammerman and L. L. Cavalli-Sforza, *The Neolithic transition and the genetics of populations in Europe* (Princeton University Press, Princeton, 1984).
- [7] A. Okubo and S. A. Levin, *Diffusion and ecological problems* (Springer, Berlin, 2001).
- [8] J. Fort and V. Méndez, Time-delayed theory of the Neolithic transition in Europe, *Physical Review Letters* 82, 867-870 (1999).
- [9] J. Fort, J. Pérez-Losada and N. Isern, Fronts from integro-difference equations and persistence effects on the Neolithic transition, *Physical Review E* 76, 031913, 1-10 (2007).

- [10] H. F. Weinberger, in *Linear partial differential equations and applications*, edited by J. Chadam (Springer, Berlin, 1978).
- [11] J. S. Clark, Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American naturalist* 152, 204 (1998).
- [12] J. Fort, Fronts from complex two-dimensional kernels: theory and application to Reid's paradox, *Journal of Applied Physics* 101, 094701, 1-7 (2007).
- [13] R. Pinhasi, J. Fort and A. J. Ammerman, Tracing the origin and spread of agriculture in Europe, *PLoS Biology* 3, 2220-2228 (2005).
- [14] M. P. Hassell, O. Miramonts, P. Rohani and R. M. May, *Journal of Animal Ecology* 64, 662-664 (1995).
- [15] S. Harris, Traveling waves with dispersive variability and time delay, *Physical Review E* 68, 031912, 1-5 (2003).
- [16] V. Méndez, V. Ortega-Cejas and D. Campos, Front propagation in population dynamics with dispersive variability and delayed growth, *Physica A* 367, 283-292 (2005).
- [17] M. Gkiasta, T. Russell, S. Shennan and J. Steele, Neolithic transition in Europe: the radiocarbon record revisited. *Antiquity* 77, 45-62 (2003).
- [18] J. Zilhao, Radiocarbon evidence for maritime pioneer colonization at the origins of farming in west Mediterranean Europe, *Proceedings of the National Academy of Sciences of the U.S.* 98, 14180-14185 (2001).
- [19] J. Fort, Population expansion in the western Pacific (Austronesia): a wave of advance model. *Antiquity* 77, 520-530 (2003).
- [20] T. D. Price, The arrival of agriculture in Europe as seen from the North, in *The widening harvest* (ed. A. J. Ammerman and P. Biagi), Archaeological Institute of America, Boston, 2003, pp. 273-294.
- [21] V. Ortega-Cejas, J. Fort, V. Méndez, Time-delayed predator-prey & competition wavefronts, *Physica A* 366, 299-307 (2006).
- [22] G. J. Ackland, M. Signitzer, K. Stratford and M. H. Cohen, Cultural hitchhiking on the wave of advance of beneficial technologies, *Proceedings of the National Academy of Sciences of the U.S.* 104, 8714-8719 (2007).
- [23] J. Fort, J. Pérez-Losada, J. J. Suñol, L. Escoda and J. M. Massaneda, Integro-difference equations for interacting species & the Neolithic transition, submitted (2008).
- [24] K. Davison, P. Dolukhanov, G. R. Sarson and A. Shukurov, The role of waterways in the spread of the Neolithic, *Journal of Archaeological Science* 23, 641-652 (2006).
- [25] J. Fort and T. Pujol, Time-delayed fronts from biased random walks, *New Journal of Physics* 9, 234, 1-14 (2007).
- [26] J. Fort, D. Jana D and J. M. Humet, Multidelayed random walks. Theory and application to the Neolithic transition in Europe, *Physical Review E* 70, 031913, 1-6 (2004).

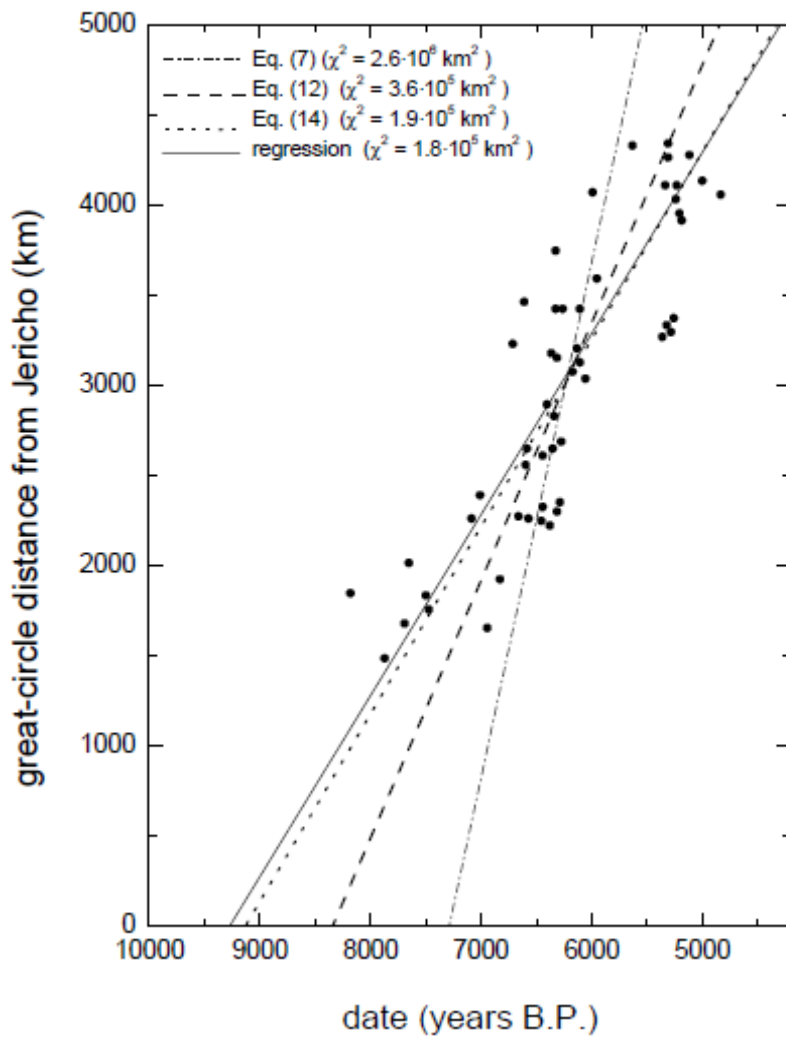
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Fig. 1 Comparison between observations (from archaeology) and predictions (from mathematical models), after [8]. The data points (one per archaeological site) and their principal-axis regression are from Ammerman and Cavalli-Sforza [4,6]. The time-delayed model, equation (14), gives a better agreement with the data (i.e., a slower rate of spread) than the non-delayed models corresponding to equations (7) and (12).

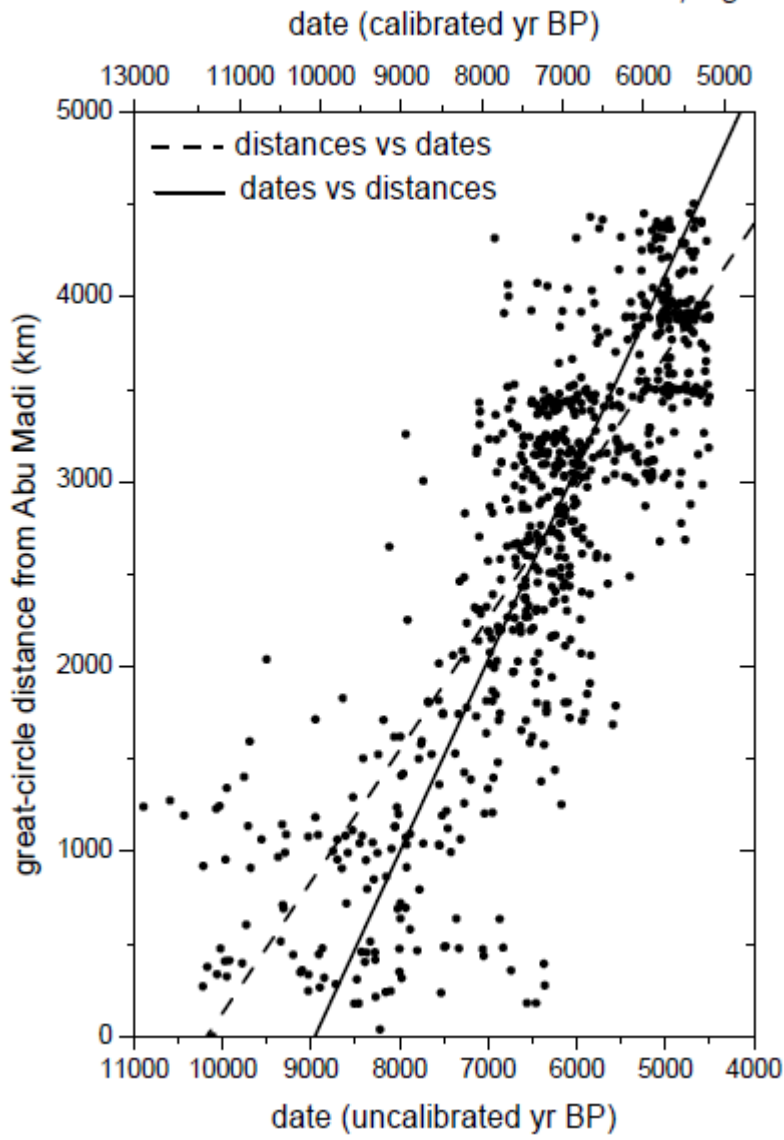
Fig. 2.a Computation of the speed range using 735 sites, after [13]. As in figure 1, great-circle distances have been used. The speed implied by the distance-versus-time regression (dashed line) is its slope, namely 0.71 ± 0.04 km/yr. The speed implied by the time-versus-distance regression (full line) is the inverse of the corresponding slope, namely 1.04 ± 0.05 km/yr (95% confidence intervals). Therefore, we estimate the overall speed range as 0.7–1.1 km/yr.

Fig. 2.b The straight lines are regression fits to 735 sites (the same lines as in Fig. 2.a). However, only sites in Denmark from Fig. 2.a are replotted here (38 data points). A consistent delay shows up in this region, because most sites are to the right (more recent dates) of the regression lines. Further mathematical models are necessary to describe this observation.

Fort, Fig. 1



Fort, Fig. 2a



Fort, Fig. 2b

