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Journal of Archaeological Science xxx (2012) 1

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Highlights

► Mesolithic populations limited the Neolithic population growth. ► Competence for space and resources is the main cause for the Neolithic slowdown. ► Dispersal restrictions alone cannot explain the Neolithic slowdown.

0305-4403/$ – see front matter © 2012 Published by Elsevier Ltd.
http://dx.doi.org/10.1016/j.jas.2012.06.027

Journal of Archaeological Science xxx (2012) 1–6

Contents lists available at SciVerse ScienceDirect

Journal of Archaeological Science

journal homepage: http://www.elsevier.com/locate/jas

Modelling the effect of Mesolithic populations on the slowdown of the Neolithic transition

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A R T I C L E I N F O

Article history:
Received 7 March 2012
Received in revised form
6 June 2012
Accepted 8 June 2012

Keywords:
Neolithic transition
Slowdown of Neolithic expansion
Northern Europe
Neolithic–Mesolithic interaction
Reaction–diffusion equations

PACS:
87.23.Cc
89.20.-a
89.65.Ef

A B S T R A C T

The expansion of the Neolithic transition in Europe took place gradually from the Near East across the whole continent. At Northern Europe, observations show a slowdown in the speed of the Neolithic front in comparison to other regions of the continent. It has been suggested that the presence of high population densities of hunter-gatherers at the North could have been the main cause for this slowdown. This proposal has recently been described by a mathematical model that takes into account: (i) the resistance opposed by the Mesolithic populations to the advance of Neolithic populations in their territory, and (ii) a limitation on the population growth dynamics due to the competition for space and resources. But these two effects are not equally responsible for the slowdown of the spread. Indeed, here we show that the limitation on the population growth dynamics seems to have been the main cause of the delay of the expansion of farming in Northern Europe.

1. Introduction

The Neolithic transition in Europe spread form the Near East to the rest of the continent between 9000 and 5000 years ago. At a continental scale, the spread of farming in Europe can be regarded mainly as taking place at an approximately constant rate (Ammerman and Cavalli-Sforza, 1971; Gkiasta et al., 2003; Pinhasi et al., 2005). However, when studying the spread at a lower scale there obviously are some regional variabilities (see, e.g., Bocquet-Appel et al., 2008). Datings of early Neolithic sites show that, for example, the adoption of agriculture at Northern Europe took place later than what one would have expected from the rates of spread of the Neolithic transition observed at other regions in the continent. This slowdown on the rate of expansion has been quantified in Isern and Fort (2010, 2011) by analyzing the areas invaded by farmers in 250 year intervals within the region delimited in Fig. 1 (this map has been constructed with 765 early Neolithic dates collected by Pinhasi et al., 2005).

According to some authors (e.g., Price, 2003; Zvelebil and Rowley-Conwy, 1984), the main reason for this slowdown seems to be the fact that, at Northern Europe, the density of established Mesolithic populations was significantly higher. According to Zvelebil and Rowley-Conwy (1984), the development of reliable hunter-gathering coastal economies allowed this increase in Mesolithic population densities at the regions near the North Sea that would have slowed down the spread of farming. In any case, whatever the reason, Price (2003) also observed that Mesolithic population densities were higher at the North. Indeed, this trend has been recently quantified (see Isern and Fort, 2011, Fig. 1 and note 4). In principle, another possible cause for the decrease in the rate of spread of agriculture could have been the climatic adaptation of domestic crops. However, the soils at Northern Europe are fertile and usable for agriculture (Zvelebil and Rowley-Conwy, 1984) and archaeological remains show that the crops that were not productive enough at colder regions were simply dropped in favour of those more productive crops (Coward et al., 2008). Therefore, a strong effect of a delay time due to climatic adaptation is unlikely. Thus, it is reasonable to develop models in order to quantify the effect of the higher presence of Mesolithic populations at Northern regions on the slowdown of the Neolithic expansion (Isern and Fort, 2010, 2011).

Reaction–diffusion models have been widely applied to study the expansion of the Neolithic in Europe. The first attempt to mathematically model the spread of agriculture in Europe was put

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http://dx.doi.org/10.1016/j.jas.2012.06.027

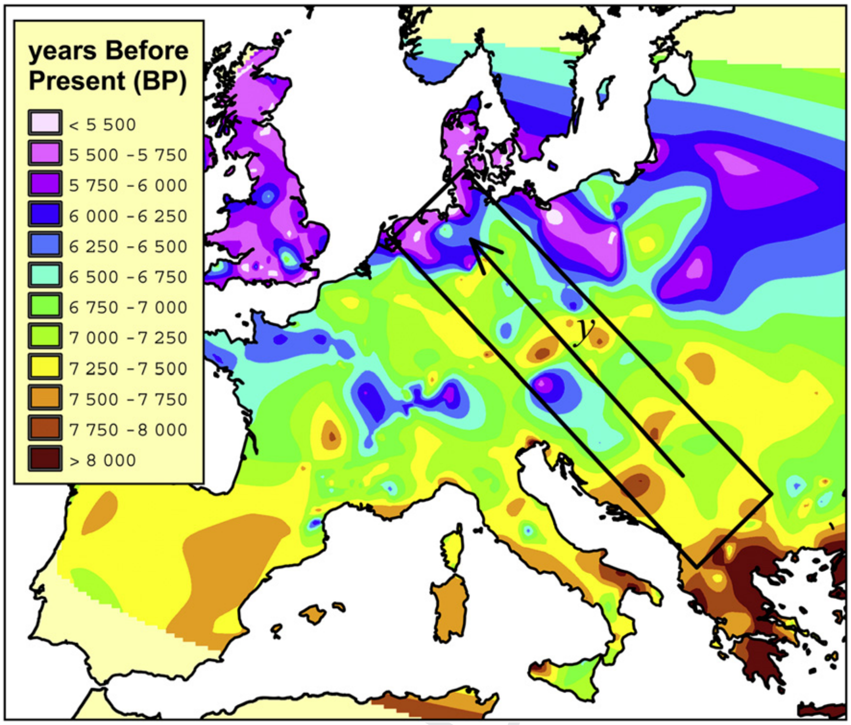

Fig. 1. Map of arrival times of the Neolithic transition in Europe. The rectangle defines the region selected to study the slowdown of the Neolithic spread at the North, along the direction indicated by the arrow. This also defines the direction *y*.

forward by Ammerman and Cavalli-Sforza (1973) with their 'wave-of-advance' model, which predicts an expansion taking place at a constant rate in a homogeneous space. More complex reaction–diffusion models developed since then take into account, e.g., the effect of encountering other populations (Isern and Fort, 2010, 2011), geographic non-homogeneities (Ackland et al., 2007), enhanced dispersions along waterways (Davison et al., 2006), etc.

Two recent papers (Isern and Fort, 2010, 2011) have proposed reaction–diffusion models for the slowdown of the Neolithic transition in Europe, taking into account the opposing effect to the spread of farming due to the presence of forager populations. These models can predict the slowdown with reasonable success, and the best representation so far is described by the following reaction–diffusion equation (Isern and Fort, 2011),

$$\frac{\partial N}{\partial t} = \tilde{a}N + 2D\left(1 + T\tilde{a}\right)\frac{\partial M/\partial y}{M_{max} - M}\frac{\partial N}{\partial y} + D\left(1 + T\tilde{a}\right)\left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2}\right), \quad (1)$$

where $N(x,y,t)$ represents the population density (individuals per km^2) of early farmers (Neolithic) at each position (x,y) and instant of time t, whereas $M(y)$ is the hunter-gatherer (Mesolithic) population density at each position at the arrival of the farming populations. Note that, for the sake of simplicity, it is assumed that M depends only on y but not x in the rectangle defined in Fig. 1 (Isern and Fort, 2010, 2011). M_{max} is the maximum density of hunter-gatherer populations that is sustainable in the region considered (rectangle in Fig. 1), D is the diffusion coefficient, T is the generation time and $\tilde{a} \equiv a(1 - M/M_{max})$ with a the intrinsic growth rate for agricultural populations (Isern and Fort, 2010). Eq. (1) is valid only at the leading edge of the front, i.e., for $N \simeq 0$ (Isern and Fort, 2011).

The reaction–diffusion Eq. (1) gives the evolution in time of the density of Neolithic individuals N (at every instant and position) by taking into account the existence of Mesolithic populations, which modify both the reaction or population growth (reproduction minus deaths) process as well as the diffusive (migratory) process. These modifications have been previously derived by considering the reduction of the free space available for Neolithic populations to settle and grow in number when moving towards already populated regions. Then, with M the density of Mesolithic populations and M_{max} the maximum sustainable density, the ratio M/M_{max} gives an idea of the degree of occupation of a certain region and, as a result, the fraction of free space available for Neolithic populations to settle at the very beginning of the Neolithization is given by the following expression (Isern and Fort, 2010)

$$s(x,y) = 1 - \frac{M(x,y)}{M_{max}}. \quad (2)$$

Now, regarding the population growth process, for low population densities it is generally considered to be exponential and characterized by the intrinsic growth rate a (Murray, 2002). However, for a region which is already populated by other human beings, the capacity of the farming populations to grow in number will be reduced due to the limitation of the free space available. This is reflected in Eq. (1) through the use of $\tilde{a} \equiv a(1 - M/M_{max})$, where a appears multiplied by the free space s (see Eq. (2)) thus yielding lower growth rates for the Neolithic populations when the rate of available space s is lower, i.e., when the density of Mesolithic population is higher (see Isern and Fort, 2011, for the detailed calculations leading to Eq. (1)).

On the other hand, the Mesolithic populations also affect the diffusion process by opposing a resistance to the Neolithic populations penetrating their territories, and this resistance can be assumed to be proportional to the degree of occupation of each region. This is taken into account mathematically using a non-homogeneous dispersion probability pattern that assigns lower probabilities to migrate towards regions with higher densities of

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Mesolithic populations, i.e., lower rates of free space (see Isern and Fort, 2010, Eqs. (2)–(5)). This leads to the second term on the right-hand side in Eq. (1). This term is inversely proportional to the fraction of free space s, i.e., the resistance to advance in the direction y is higher when less space is available; and is proportional to $\partial M/\partial t$, which means that the resistance is higher when the increase in population density is abrupt (see Isern and Fort, 2011, for the detailed calculations leading to Eq. (1)).

The front speed can be obtained from Eq. (1) through linear and variational analyses (see Méndez et al., 1999), which lead to the following expression (Isern and Fort, 2011)

$$c = \sqrt{4D\tilde{a}\left(1+T\tilde{a}\right)} - 2D\left(1+T\tilde{a}\right)\frac{\partial M/\partial y}{M_{\max}-M}. \qquad (3)$$

Note that this expression for the front speed does indeed include both effects caused by the hunter-gatherer populations explained above: (i) Eq. (3) contains the modified growth rate $\tilde{a}$, which yields lower speeds for higher values of M, and (ii) the last term in Eq. (3) clearly comes from the second term on the right-hand side in Eq. (1), and diminishes the front speed when M is high ($M \rightarrow M_{\max}$) and/or when M grows rapidly (high values of $\partial M/\partial y$).

So, the model described by Eq. (1) corresponds to a scenario where the presence of hunter-gathering populations has two effects that decrease the rate of expansion of the Neolithic populations, namely (i) a resistance to the immigration of farmers, and (ii) a limitation of their population growth dynamics (Isern and Fort, 2011). But, are both effects equally significant? Bellow we will describe two different scenarios, each considering only one of both effects, in order to study the relative importance of them on the slowdown of the Neolithic wave of advance in Northern Europe.

2. Theory

2.1. Reduced forward dispersion

We will first consider a situation in which the presence of Mesolithic populations has an important effect only on the dispersion, or migration, process (effect (i) at the end of Section 1), whereas the effect on the population growth process (effect (ii)) will be considered negligible in this subsection. In modelling terms, this means that we will consider a non-homogeneous diffusion probability pattern, with the probability to move towards each direction proportional to the available space $s = (1 - M/M_{\max})$ (Eq. (2)) in the considered direction; so, the reaction–diffusion equation describing this situation will still have the second term on the right-hand side in Eq. (1). The population growth dynamics, however, will no longer be characterized by the modified growth rate $\tilde{a}$ but by the intrinsic growth rate a, as this scenario considers the effect on the population growth to be negligible. Then, the reaction–diffusion model would be

$$\frac{\partial N}{\partial t} = aN + 2D(1+Ta)\frac{\partial M/\partial y}{M_{\max}-M}\frac{\partial N}{\partial y} + D(1+Ta)\left(\frac{\partial^2 N}{\partial x^2}+\frac{\partial^2 N}{\partial y^2}\right). \qquad (4)$$

Note that, as already reasoned above, the main difference between Eqs. (1) and (4) is that in Eq. (4) a appears instead of $\tilde{a}$.

In a system governed by Eq. (4) the front speed can be calculated by analytical and variation analyses (see Méndez et al., 1999) and is given by the following expression

$$c = \sqrt{4Da(1+Ta)} - 2D(1+Ta)\frac{\partial M/\partial y}{M_{\max}-M}, \qquad (5)$$

which is similar to Eq. (3) but, as could be expected for this scenario, $\tilde{a}$ has been substituted by a. The front speed described by Eq. (5) decreases when the Mesolithic population density is high, due to the negative contribution of the last term in this expression.

2.2. Limited population growth

Here, conversely, we will consider that the main effect on the Neolithic population dynamics due to encountering Mesolithic populations is the competition for the space and resources once settled, and thus, we will consider a limitation on the population growth process proportional to the available space s (effect (ii) at the end of Section 1). Then, in this scenario the slowdown will not be caused by the hunter-gathering populations having a direct effect on the migration (effect (i) at the end of Section 1). Mathematically this means that population growth will be characterized by the modified growth rate $\tilde{a}$, as in Eq. (1). The diffusion, on the other hand, will now be an isotropic process because, as the presence of hunter-gatherers will have no effect on the migration, the diffusion will be equally probable in all directions (i.e., the effect (i) at the end of Section 1 is now neglected). Therefore, the second term on the right-hand side of Eq. (1) will not appear in this scenario. Then, this system can be described by the following equation

$$\frac{\partial N}{\partial t} = \tilde{a}N + D\left(1+T\tilde{a}\right)\left(\frac{\partial^2 N}{\partial x^2}+\frac{\partial^2 N}{\partial y^2}\right). \qquad (6)$$

Again, a system governed by such equation will generate an expanding front whose speed can be obtained from the following expression,

$$c = \sqrt{4\tilde{a}D\left(1+\tilde{a}T\right)}, \qquad (7)$$

which has been calculated from Eq. (6) by means of linear and variational analyses (see Méndez et al., 1999). Note that the fact that now the diffusion is homogeneous entails that the last term in Eq. (3) no longer appears here. Nonetheless, Eq. (6) does also predict a reduction of the front speed when the Mesolithic population density M grows, because $\tilde{a} = a(1 - M/M_{\max})$ is lower when M approaches $M_{\max}$.

2.3. Parameter values

In order to analyze the results from the models described above we need to assign numerical values to the different parameters. For the Neolithic parameters (a, D and T) we will use typical values that are usually applied when modelling the Neolithic expansion in Europe, and which have been obtained from the analysis of preindustrial farming populations anthropological data. We will thus use an intrinsic growth rate for farmer populations $a = 0.028$ yr^{-1} (Isern et al., 2008), a generation time $T = 32$ yr (Fort et al., 2004) and a diffusivity $D \simeq 11.96$ km^2 yr^{-1} ($D = 1531/4T$ km^2 (Fort and Méndez, 1999)). These are also the same values that were previously used when studying the model in Isern and Fort (2011) (and summarized in the Section 1 of the present paper).

In addition to the anthropological data for the Neolithic populations, in order to apply the models above it is also necessary to have a function for the Mesolithic population density in space $M(y)$. Ideally, we would need to know the evolution of the Mesolithic population in space and time, in order to know the exact population density at every position upon the arrival of the Neolithic populations; however, there is not enough available data to make such precise estimations, so we will just use a stationary approximation for the Mesolithic population density at the Neolithic arrival time, $M(y)$. In fact, only the reduced Mesolithic population density

$M(y)/M_{\max}$ is necessary, and this was estimated by Isern and Fort (2011) using data on the relative density of Mesolithic sites from the data on the INQUA database (Vermeersch and Boon, 2010). The best fit to these data, for the region delimited in Fig. 1 is

$$M/M_{\max} = \frac{1}{1 + B\exp(-y/\tau)}, \tag{8}$$

with $B = 144.30728$ and $\tau = 163.39869$ km. This equation describes a distribution of the Mesolithic population density with very low densities at the South (within the region delimited in Fig. 1), and which increases along the y-direction following an *S*-shaped curve that reaches the maximum value at the Northern region (see Isern and Fort, 2011, Fig. 1).

3. Results

In this section we present the results obtained from the two *partial* models for the slowdown of the Neolithic transition obtained in the previous section, and compare them to the *complete* model from Isern and Fort (2011) (Eq. (1) in this paper) and to the observational data. These comparisons will allow us to study the relative importance of the two modifications introduced in the Neolithic population dynamics (in Eq. (1)) as a result of the interaction with Mesolithic populations.

Fig. 2 shows how the rate of spread of the Neolithic transition changes when expanding from the Balkans to the North Sea, according to the different models (lines) and the observational data (squares), as computed by Isern and Fort (2011) from the database by Pinhasi et al. (2005). The solid line in Fig. 2 corresponds to the *complete* model (Eq. (3)), that is, the model that includes both effects of the Mesolithic populations: (i) reducing the diffusion forwards, and (ii) limiting the population growth. The other two lines correspond to the *partial* models developed in this paper, with the dotted line corresponding to the reduced-diffusion model described in Section 2.1, Eq. (5), and the dashed line to the model with limited population growth dynamics described in Section 2.2, Eq. (7).

Both models developed in this paper predict a decrease of the Neolithic spreading speed when approaching Northern regions

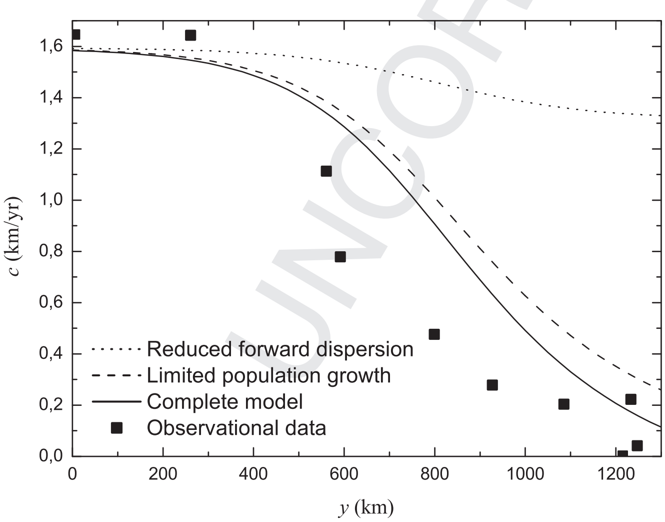

Fig. 2. Predictions for the slowdown of the Neolithic transition due to encountering Mesolithic populations when considering a reduction in forward dispersion (dotted line, Eq. (5)), a limited population growth (dashed line, Eq. (7)), or both modifications (solid line, Eq. (3)). Symbols correspond to the observed front speeds measured from the Balkans to the North Sea (rectangle in Fig. 1).

(large values of y), but this decrease is not equally important for both models. Comparing the results in Fig. 2 we see that the model with limited population growth (dashed line) predicts an important slowdown on the rate of spread, close to the prediction obtained from the *complete* model (solid line). In contrast, the model that only takes into account the reduced forward dispersion (dotted line) predicts a rather slight slowdown, in comparison with the results from the *complete* model.

All of the results presented in this section have been calculated with the parameter values defined above and for the region delimited in Fig. 1, so the y coordinate in Fig. 2 represents the positions along the y-direction as indicated in Fig. 1.[1]

4. Discussion

The models developed in this paper implicitly assume that the spread of farming in the rectangle in Fig. 1 was mainly a demic process, i.e., that cultural diffusion was of comparatively little importance. It is very interesting that Shennan and Edinborough (2007) have reached the same conclusion directly from archaeological data, which show very rapid increases in Neolithic population densities as well as comparatively very small values of pre-existing Mesolithic population densities. Genetic data also support a mainly demic process, both on the basis of DNA from modern European populations (Chiki et al., 2002) and from ancient remains (Haak et al., 2010; Skoglund et al., 2012). However, it is important to stress that it is not possible to compare mathematical models of the spread rate directly to genetic data, because the latter refer to the geographic distribution of genes and do not yield any information on the front speed.

Some models of Neolithic spread (Ammerman and Cavalli-Sforza, 1971; Fort and Méndez, 1999) are gradual, in the sense that they predict a constant spread rate. Instead, the models in the present paper display an additional level of complexity, leading to a slowdown of the Neolithic spread rate. We have mathematically introduced this slowdown by assuming that the interaction with Mesolithic populations either reduced the probability for Neolithic populations to move forwards or limited their population growth dynamics. These two effects had already been considered as a single item in Isern and Fort (2011), but by studying them separately we can, not only see that a high presence of Mesolithic populations can indeed be that cause for the slowdown of the Neolithic expansion, but also infer on which was the most important mechanism that caused this slowdown. According to the results in Fig. 2, from the two ways in which the presence of Mesolithic populations can induce a slowdown on the expansion of the Neolithic transition, as considered in Eqs. (1) and (3) (Isern and Fort, 2011), the most important one is the limitation in the population growth dynamics due to the competition for space and resources. This can be concluded from the fact that the model in which only the limitation in population growth is considered (Eq. (7) and dashed line in Fig. 2) does practically reproduce the results from the model including both effects (Eq. (3) and solid line in Fig. 2).

In addition, if comparing the results from the two *partial* models with the observational data (symbols in Fig. 2), the model including only the effect on the population growth process, Eq. (7), is still able to give quite a good account of the observed speeds. Contrarily, if

[1] The origin of the y coordinate was set in Isern and Fort (2010) as the position of the centroid of the area corresponding to the period 7250–7500 Cal yr BP (yellow (in the web version) in Fig. 1), so the lower edge of the rectangle corresponds to $y = -385$ km. The earlier periods (region bellow and to the right of the rectangle) are not considered due to the additional sea travel effect (Isern and Fort, 2010).

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only taking into account the reduced forward diffusion due to encountering hunter-gatherer populations, Eq. (5), the prediction differs substantially from the observations.

Thus, according to our results, the slowdown of the Neolithic in Europe can be explained by the presence of high densities of Mesolithic populations in Northern Europe and the main mechanism in hindering the Neolithic expansion would have been through the limitation in the population growth dynamics due to competition for space and resources. As far as we know, the available data on the Neolithic transition is not detailed enough as to verify these results, but it is interesting to note that a slow population growth dynamics would agree with the long coexistence period between farmer and hunter-gatherer populations before the complete substitution that has been observed at Northern Europe (Zvelebil and Rowley-Conwy, 1984; Price, 2003; Malmer, 2002). Nonetheless, our models are only valid at the leading edge of the expanding front, i.e., when the Neolithic population density is very low, and cannot be applied to predict the dynamics behind said front. Other authors have developed more complex models to study the interaction between farmer and hunter-gatherer populations behind the front for other locations (such as India (Patterson et al., 2010) or the evolution along a river valley (Fedotov et al., 2008)), and some of their hypothesis could be adapted to be applied in this case, however this would lead to a more complicated equations system that would have to be solved with computational methods.

The simplicity of our models makes it possible to make only a few, clear assumptions, and not to use parameter values or hypothetical functions that cannot be directly estimated from anthropological or archeological data. However, it is true that the local details of the Neolithic spread (Fig. 1) are still more complex than single-coordinate models such as those analyzed here. More detailed descriptions cannot be based on analytical approaches such as those presented in the present paper, but will require numerical simulations in real geographies.

Finally, we want to add a comment on the parameters used in the present paper. The value of the initial growth rate a used here has been estimated from ethnographic data of human populations settling in previously empty space (Isern et al., 2008). However, Guerrero et al. (2008) have performed estimations of a directly from archaeological data based on the rise in fertility (detected as a rise in the proportions of immature skeletons in early Neolithic cemeteries) and a sample of 45 reference historic life tables. In this way they have estimated $a = 0.024$ yr^{-1}, which is very close to the value $a = 0.028$ yr^{-1} applied in our paper based on ethnographic observations (Isern et al., 2008). On the other hand, as far as we know, the values of the generation time T and the diffusion coefficient D have not yet been estimated directly from archaeological data.

5. Conclusions

In this paper we have developed two reaction–diffusion models for the slowdown of the Neolithic transition based on a previously published model (Isern and Fort, 2011) that considered the high presence of Mesolithic populations at the North as the main cause for the slowdown. Each new model takes into account only one of the two effects assumed by Isern and Fort (2011), i.e., (i) one model assumes that the presence of Mesolithic populations affects the Neolithic population dynamics by hindering their dispersion towards the more populated regions, while (ii) the other model considers that the competition for space and resources between both populations limits the capacity of the Neolithic populations to grow in number.

From the comparison between models we have obtained a new result, namely, that the limitation in the population growth dynamics is the most important effect, i.e., that it predicts a more important slowdown on the rate of expansion of the Neolithic transition in Northern Europe. Thus, according to our models, the main way in which the Mesolithic populations reduced the rate of spread of farming seems to have been the fact that, in regions where the density of hunter-gathering populations was high, their use of space and resources would have limited the capability of Neolithic populations to grow in number, which would have led in turn to a lower number of individuals who migrate (and diffuse the Neolithic culture). Contrarily, the resistance to the migration of farmer populations as a direct result of the presence of Mesolithic populations seems to have had a much less important effect.

Acknowledgements

We are thankful to J.-P. Bocquet-Appel for discussions on archaeological estimations of the initial growth rate a. Funded by the Ministry of Science (grants SimulPast-Consolider-CSD-2010-00034 and FIS-2009-13050) and the Generalitat de Catalunya (Grup Consolidat 2009-SGR-374).

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Please cite this article in press as: Isern, N., Fort, J., Modelling the effect of Mesolithic populations on the slowdown of the Neolithic transition, Journal of Archaeological Science (2012), http://dx.doi.org/10.1016/j.jas.2012.06.027

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Please cite this article in press as: Isern, N., Fort, J., Modelling the effect of Mesolithic populations on the slowdown of the Neolithic transition, Journal of Archaeological Science (2012), http://dx.doi.org/10.1016/j.jas.2012.06.027