Demographic model of the Neolithic transition in Central Europe

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ABSTRACT – *Several recent lines of evidence indicate more intensive contact between LBK farmers and indigenous foragers in Central Europe (5600–5400 calBC). Strong continuity has been identified between Mesolithic and Neolithic material cultures; faunal assemblages, and isotopic analyses of diet have revealed a greater role of hunting in LBK communities; genetic analyses have suggested that the modern Central European gene pool is mainly of Palaeolithic origin. Surprisingly little attention has been paid to demographic aspects of the Neolithic transition. In our study, demographic simulations were performed to assess the demographic conditions that would allow LBK farmers to spread across central Europe without any admixture with Mesolithic foragers. We constructed a stochastic demographic model of changes in farming population size. Model parameters were constrained by data from human demography, archaeology, and human ecology. Our results indicate that the establishment of farming communities in Central Europe without an admixture with foragers was highly improbable. The demographic conditions necessary for colonization were beyond the potential of the Neolithic population. Our study supports the integrationists' view of the Neolithic transition in Central Europe.*

IZVLEČEK – *Več novih dokaznih linij kaže na intenzivnejše stike med LKB poljedelci in prvotnimi nabiralci v srednji Evropi (5700–5500 calBC). Dognana je bila možna kontinuiteta med mezolitskimi in neolitskimi materialnimi kulturami; favnistični zbiri in izotopske analize prehrane kažejo večjo vlogo lova v LBK skupnostih; genetske analize kažejo, da je moderni srednje evropski genetski fond pretežno paleolitskega izvora. Presenetljivo malo pozornosti je bilo posvečene demografskim aspektom neolitizacije. V naši študiji uporabljamo demografske simulacije, da bi ocenili demografske pogoje, ki bi omočili LKB poljedelcem širitev preko srednje Evrope brez kakršnegakoli mešanja z mezolitskimi nabiralci. Oblikovali smo stohastični demografski model sprememb v velikosti poljedelske populacije. Parametri modela so bili izvedeni iz podatkov o humani demografiji, arheologiji in humani ekologiji. Naši rezultati kažejo, da je bila ustanovitev poljedelskih skupnosti brez mešanja z nabiralci malo verjetna. Demografski pogoji potrebni za kolonizacijo so presegali potencial neolitske populacije. Naša študija podpira integracionistični pogled na neolitizacijo v srednji Evropi.*

KEY WORDS – *demographic simulations; Neolithic transition; Central Europe; colonization; fertility; population growth*

Introduction

The pattern of the introduction of domesticated plants and animals into Europe has been a subject of major interest for more than one hundred years (*Gronenborn 2007*). Although it is generally accepted that farming spread into Europe from the Near East, disagreements prevail about the relative contribution of Near Eastern farmers and indigenous foragers to the establishment of farming communities. Three alternative explanations of the spread of agriculture across Europe have been proposed, which were summarized by Zvelebil (*2000*) as the migrationist, indigenist, and integrationist positions. Migra-

tionists favor the spread of farmers, with the genetic replacement of Mesolithic foragers; indigenists prefer the spread of farming with no genetic contribution from the Near East; and integrationists emphasize both people and ideas, and presume a genetic admixture of foragers and farmers.

Recently, it has become clear that the spread of agriculture across Europe cannot be modeled monocausally. The spread involved a variety of mechanisms that were shaped by regional conditions. On the one hand, local Mesolithic groups played a significant role in the spread of agriculture throughout much of Northern Europe, the Alps, the Atlantic fringe of France and Central Iberia. On the other hand, the Eastern Mediterranean and South-Eastern Europe are regions that probably experienced farmer migration (*Zvelebil 2000; Robb and Miracle 2007*). Similarly, the spread of farming across Central Europe has traditionally been accepted as an example of agricultural colonization by farmers of Linear Pottery Culture (LBK) (*Childe 1925; Piggott 1965; Vencl 1986; Lüning 1988; Price et al. 1995; Bogucki 2001; Neustupný 2004*). It is believed, that LBK farmers spread within 4–6 generations from its origin in Western Hungary over the broad area extending from Western Ukraine to the Rhine River in Germany (Fig. 1). Recently, the migrationist view that the LBK spread across Central Europe has been challenged and, today, the integrationist view is accepted by the majority of scholars from continental Europe concerned with the Central Early Neolithic (*Gronenborn 2007*).

The integrationist position is supported by a number of indicators of contact between foragers and farmers. Typological and technological analyses of lithic assemblages show a continuity in stone tool production from the Mesolithic to the Earliest LBK (*Gronenborn 1998; Kind 1998*). Some Earliest LBK sites yield relatively high amounts of game, which might be interpreted as an interaction between Earliest LBK and Mesolithic groups (*Gronenborn 1999*). Also, stable isotope analyses of LBK skeletons from Southern
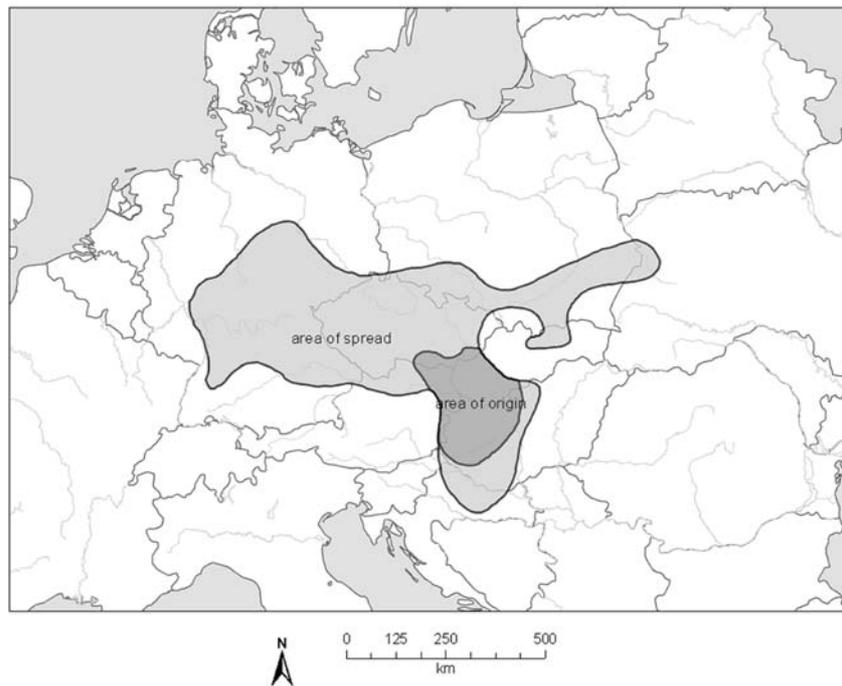

Fig. 1. Map of the LBK origin area in Western Hungary (dark grey) and the area settled after the Earliest LBK expansion over Central Europe from 5600 to 5400 calBC (light grey). Adapted from Zvelebil (2001.Fig. 2).

German have demonstrated relatively high stable nitrogen ratio values, traditionally interpreted as a reliance on animal protein (*Dürrwächter et al. 2006*). Several authors have suggested that late Mesolithic foragers practiced some kind of small-scale farming (*Erny-Rodmann et al. 1997; Tinner et al. 2007*). Strontium isotope analyses of human skeletons from LBK cemeteries in South-Western Germany have revealed a significant amount of non-locals, which would indicate that foragers had joined LBK communities (*Price et al. 2001; Bentley 2007*). Genetic studies of the classical markers, mtDNA, and Y-chromosome, have indicated a significant contribution from Mesolithic foragers to the gene pool of modern Europeans (*Richards 2003*). The admixture view has been strengthened by the direct extraction of mtDNA from skeletons buried at LBK cemeteries in Germany and Austria (*Haak et al. 2005*).

Given the fact that many different disciplines have been involved in explaining the mechanism of Neolithic dispersal, it is surprising how little has been done in the field of demography. Authors have only generally presumed that the prerequisite of the colonization would have been a high rate of population growth (*Crubézy et al. 2002*), and LBK farmers would have had to reproduce at the rate approaching the theoretical maximum for human population. A growth rate of from 2.0% to 3.5% per year has been universally used as the input value in models of po-

pulation dynamics, such as the wave of advance model (*Ammerman and Cavalli-Sforza 1973*) and its various generalizations (*Fort and Mendéz 1999; Pinhasi et al. 2005; Davison et al. 2006; Davison et al. 2007*).

So far, there have been only a few attempts to estimate the growth and/or fertility rates of the LBK population directly from the archaeological evidence. Neustupný (*1983*) produced abridged life tables from LBK skeleton samples from eastern Germany and estimated the growth rate at 1–2%. A similar value was calculated by Petrasch (*2001*). His analysis was based on the function of exponential growth, and input variables were derived from the distribution of LBK settlements and radiocarbon data. Unfortunately, both estimates are deterministic, and do not account for the uncertainty associated with adopting input parameters from archaeological sources.

In this study, we built a stochastic demographic model that describes the demographic conditions of Neolithic transition in Central Europe. Demographic simulations were performed to directly test the colonization hypothesis. In particular, our question is whether the growth and fertility rates of Earliest LBK population could have been high enough to allow the farmers to colonize Central Europe without mixing with the local Mesolithic foragers.

Demographic model

Our model is a demographic projection of the size of the LBK population during the expansion across Central Europe. To avoid estimations of many parameters, we applied a simple mathematical solution. We modified the basic exponential equation $P_t = P_0 e^{rt}$ (*Newell 1988.182*), where P_0 and P_t are population size at the beginning and end of the expansion; t is the duration of the process in years, and r is the growth rate. The exponential curve is presented in Fig. 2. It may be seen that population size (Y axis) is a function of only two parameters: time (X axis) and growth rate (the slope of the curve).

We rearranged the basic equation describing exponential growth to obtain the growth rate $r = \ln(P_t/P_0)/t$. Because we were not able to estimate the LBK population size with sufficient accuracy, we replaced it with the product of area size and population density. The last equation was then rewritten as $r = \ln(A_t \cdot d/A_0)/t$, where A_0 and A_t are the size of the origin area and settled area respectively, and d is the ratio of population density at the end to density at the beginning of the expansion ($d = d_t/d_0$).

We then used the estimate of growth rate to measure LBK fertility. Total fertility rate (TFR), which is the number of children born to average woman, was calculated according to the equation: $TFR = e^{r \cdot g}/S \cdot l_g$ (*Hinde 2002.25*), where g is the generation length, l_g is the proportion of females surviving to g years of age, and S is the proportion of females at birth.

Values of input parameters

The values of input and output parameters of the model were obtained from archaeological, ethnographic and demographic sources. The list of input and output parameters along with their values that were entered in the simulations is presented in Table 1. In the following paragraphs we will explain in detail the determination of these values.

The size of the LBK area of origin (A_0) was computed in GIS software from four maps produced by archaeologists (*Kalicz 1993; Petrasch 2001; Zvelebil 2001; Bánffy 2004*). Similarly, the size of the area settled during the expansion (A_t) was derived from five maps of Earliest LBK site distribution (*Lüning et al. 1989; Gronenborn 1998; Bogucki 2000; Jochim 2000; Zvelebil and Lillie 2000*). To avoid regions in high altitudes we consider only part of the landscape up to 350m above sea level. This level was suggested as an upper limit of LBK settlement activity. Only a small proportion of LBK settlements have been discovered above the 350m contour (*Rulf 1983; Květina 2001*). Fig. 3 shows an example of the area restricted by the 350m contour made for a map
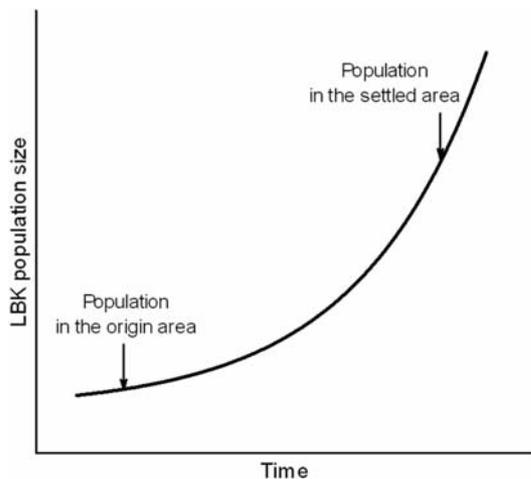

Fig. 2. Exponential growth. The function describes how changes in population size (Y axis) depended on time (X axis). Growth rate is reflected by the steepness of the curve.

of the settled area suggested by Zvelebil (*2001*). Similar maps were produced for each of the four maps of the origin area and each of the five maps of the settled area. The final input parameter estimated from archaeological data is the duration of the initial spread of Earliest LBK (*t*). Although the absolute data differ from author to author (5600–5400 calBC, *Gronenborn 1999*; 5400–5200 calBC, *Zvelebil 2004*), most agree that the spread occurred within an interval of 100–200 years.

The next three input parameters were acquired from demographic sources. The relative proportion of females at birth (*S*) and mean age at childbearing (*g*) have been assumed to be relatively stable among human populations with natural reproduction (*Hinde 2002*). So we were able to find reliable point estimates of both parameters. In all simulations, the proportion of females at birth was set to 0.4878 (100 females per 105 males) and mean age at childbearing to 27.5 years of age. Also, density ratio (*d*) was fixed in basic simulations to the single value of 100%, which means that density was assumed to remain constant during the spread of LBK.

symbol	description	n	min	max
A_o	Origin area limited by 350 m a.s.l. contour [km²]	4	32.714	51.446
A_t	Settled area limited by 350 m a.s.l. contour [km²]	5	181,978	232.45
t	Time of spread [years]	12	100	200
g	Generation length [years]	8	27.5	27.5
S	Proportion of females at birth	5	0.4878	0.4878
l_g	Proportion of females survived to the g years of age	1	0.24	0.43
d	Density ratio	1	100	100
TFR*	Total fertility rate [children per woman]	11		6.92
n: Number of estimates				

Tab. 1. List of the input parameters and the output variable (*) of the demographic model.

Estimating female mortality was not straightforward. Women's survival to the mean age at childbearing (*l_g*) was obtained from life tables. We did not rely on the life tables of real prehistoric populations because the skeletal data that the tables stem from were considered unreliable. Instead, we estimated mortality from simulated life tables which we generated using the Brass two-parametric relational system of model life tables (*Brass 1971*). The Brass logit system is based on a generic survival function which is transformed by a logit transformation into a new survival curve. By varying either of two parameters, we generated 1000 model life tables with a life expectancy at birth of between 18 and 25 years, which is assumed to be the mortality level of the prehistoric population (*Gage 2005*). Finally, women's survival to the mean age at childbearing, the input parameter of our model, was obtained from this set of simulated life tables.

Output variable and comparative sample of fertility

The only output parameter of our demographic model is a measure of the fertility of the LBK population, namely its total fertility rate (TFR). To assess the level of fertility obtained in simulations, we created the comparative sample of TFR. The comparative sample comprises TFRs of eleven recent populations with natural reproduction. Populations included in the sample are horticulturalists (extensive agriculturalist) who cultivate ce-
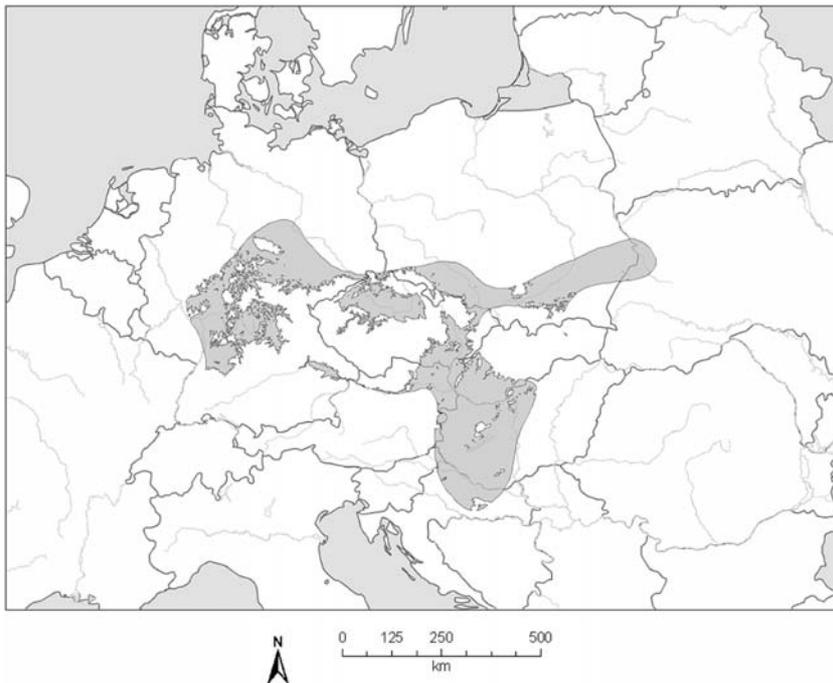

Fig. 3. Map showing the area settled by the Earliest LBK around 5400 calBC up to 350m above sea level. Base map adapted from Zvelebil (2001. Fig. 2).

reals and are sedentary. These characteristics have traditionally been attributed to the LBK population (*Gregg 1988*), although some authors have assumed that LBK cultivators were familiar with some intensive gardening techniques (*Halstead 1989; Bogaard 2004*).

TFR data were gathered from two studies concerned with the relationship between fertility and subsistence (*Bentley et al. 1993; Sellen and Mace 1997*). The histogram of TFR in the comparative sample is shown in Fig. 4. The distribution of TFR is highly skewed to larger values. Populations with TFR greater than 6 prevail in the sample. The sample maximum is 6.7 children, but to obtain the parametric maximum in the population (population in the statistical sense), we used an unbiased standard bootstrap method of confidence limits calculation (*Manly 2007*). This parametric maximum we entitle here as the critical value of TFR, and its value was calculated at 6.92 children born to the average woman. We assumed that the critical value of TFR represents the upper limit of fertility that could be attained by LBK women during the Neolithic transition.

Randomization step

Table 1 demonstrates that four out of seven input variables are defined in range. Because we did not want to reduce the interval estimates of input parameters only to a point estimate (*e.g.* average value), we inserted a randomization step into the model. The randomization step is a stochastic component of the simulations and is motivated by the complexity associated with the input parameters. The principle of the randomization step is described in Figure 5. First, a single value of each input parameter was
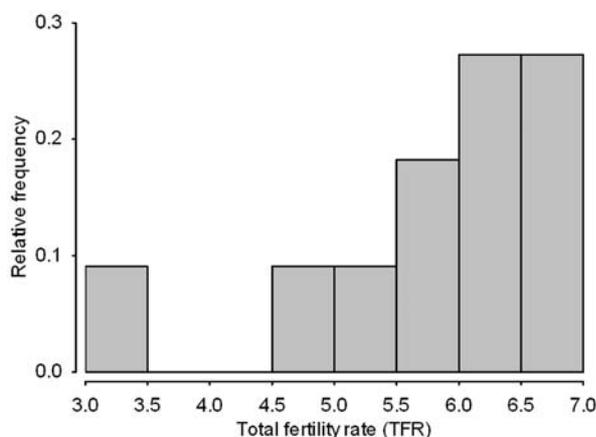
drawn at random from the interval shown in Table 1. These values were used to calculate the output variable, *i.e.* TFR. Then, a process of random sampling of input parameters and calculation of output variable was run 10 000 times. In the end, we obtained 10 000 estimates of TFR. Each of the 10 000 iterations of the model represented one possible demographic scenario of the Neolithic transition in Central Europe.

Statistical and graphic analyses (descriptive statistics, multivariate regression, randomization analysis) were performed in MS Excel 2003 (© Microsoft Corporation, 1985–2003) and STATISTICA 6.1 (© StatSoft, 1984–2003). 3D surface charts were made in R software (*Ihaka and Gentleman 1996*), version 2.8.0 (© 2008 The R Foundation for Statistical Computing). Geographical data were analyzed in ArcMap 9.0 (© ESRI, 1999–2004).

Results

The descriptive statistics of 10 000 estimates of TFR and growth rate obtained in the simulations are shown in Table 2. The growth rate of the farming population ranges from 0.64% to 1.96% per year. The estimates of total fertility rates oscillate from around 6 to 13 children per woman. The distribution of TFR is skewed (Fig. 6); lower values (up to 9 children) are more frequent in the simulations than larger values. From both Table 2 and Fig. 6 it is evident that the majority of iterations give an estimate of TFR greater than the critical value of fertility. In fact, only 7.89% of TFR estimates are lower than the
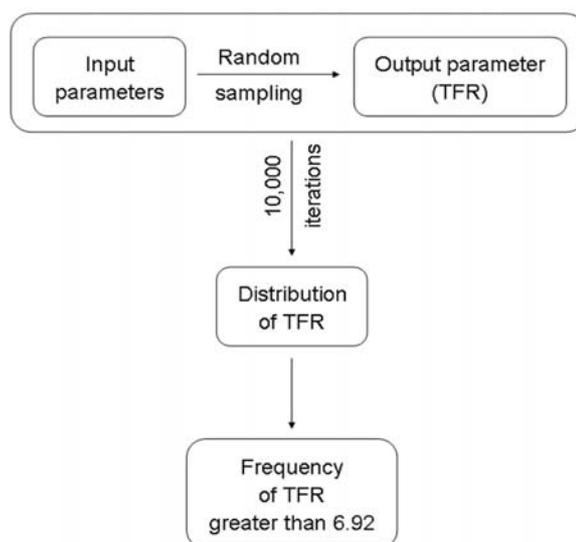

Fig. 4. The distribution of total fertility rate (TFR) in the comparative sample (n = 11 horticulture societies).

Fig. 5. The principle of the demographic model with a randomization component (see text for the explanation).

critical value of 6.92 children. In other words, around 92% of the demographic scenarios of the Neolithic transition in Central Europe contradict the hypothesis of colonization.

To assess the effect of input parameters, we performed a multiple regression analysis of data obtained in 10 000 iterations. As independent variables, we selected only four input parameters that are defined in range: origin area, settled area, time and survival of females (see Tab. 1). The remaining input parameters were excluded from the regression analysis because they were estimated by single values and have, therefore, the same effect on TFR in each iteration. The analysis of residuals suggested that the regression trend in raw data is non-linear. To achieve linearity, we transformed the raw data by natural logarithm. The results of multivariate regression analysis and basic statistics of ln transformed inputs parameters are given in Table 3. Multivariate regression is highly significant ($P < 10^{-5}$). The high value of the coefficient of determination (0.996) indicates that the regression provides a good fit to the data. In fact, 99.6% of the variability of TFR is explained by the model. The standardized coefficients shown in Table 3 indicate that the greatest effects on TFR came from the duration of spread and the survival of females. On the other hand, variation in the size of the origin and settled area has minimal impact on fertility estimate.

The relationship among total fertility rate and three input parameters in the model is shown in Figure 7. The isolines in contour graphs connect points of equal value of TFR. The ratio of population density in the settled area to population density in the origin area is displayed on the X axis, and the proportion of females surviving to 27.5 years of age on the Y axis. The contour graph on the left shows the duration of LBK initial spread through Central Europe fixed to the value of 100 years, and to 200 years in the graph on the right. Both contour graphs were computed with average size of the origin and settled area. The isoline at 6.92 children represents the critical value of the total fertility rate of horticultural societies. The white parts of the graphs correspond to the fertility estimates that match the colo-
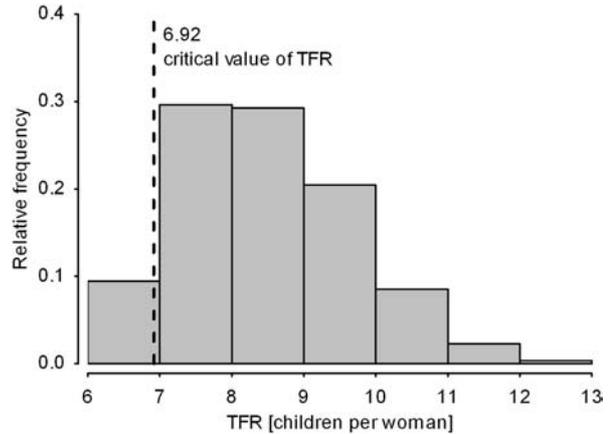

Fig. 6. The distribution of the output variable. Histogram comprises 10 000 estimates of TFR obtained in the simulations. Dashed line indicates the position of the critical value of fertility for horticultural societies (6.92 children, see text for explanation).

nization hypothesis. The grey segments represent demographic conditions that lead us to reject the colonization hypothesis. For example, the combination of 100% density, 40% survival and duration of 100 years (left contour graph) gives a TFR estimate of almost 8 children.

Discussion

In this study, we estimated the level of fertility and growth rate of the LBK population via demographic modelling. The objective was to assess whether such a level of fertility and growth rate could be high enough to allow the LBK farmers to spread across Central Europe within less than 200 years without admixture with indigenous foragers. Although both fertility and mortality levels can be estimated from skeletal remains (*Buikstra et al. 1986; Paine and Harpending 1996; Bocquet-Appel 2002*), the low number of Earliest LBK cemeteries with well preserved human remains and their non-random spatial distribution restrict such attempts. In situations where few empirical data are available, demographic simulations are a powerful tool for answering similar questions (*cf. Steele et al. 1998; Alroy 2001; Surovell 2003*).

In this study, we estimated the growth rate range of the LBK population at 0.64 to 1.96% per year (Tab. 2). Comparison with the estimates proposed by other authors suggests that such values seem to be rather high for the LBK population. Bocquet-Appel (*2002*) has even estimated that the population undergoing Neolithic transition in Europe was

	min	max	95% of values	TFR < 6.92 [%]
growth rate [%]	0.64	1.96	0.77–1.58	
TFR	5.93	13.03	6.75–10.60	7.89

Tab. 2. Descriptive statistics of 10 000 estimates of growth rate and total fertility rate obtained in the simulations.

	mean	V [%]	beta	SE$_{beta}$
origin area	10.6	1.2	−0.18	0.0006
settled area	12.2	0.6	0.10	0.0006
time	5.0	4.0	−0.46	0.0006
survival of females	−1.1	10.8	−0.87	0.0006

V: Coefficient of variation
beta: Standardized regression coefficient
SE$_{beta}$: Standard error of coefficient

Tab. 3. Effect of input parameters to output variable (TFR). Regression analysis computed after ln transformation. Coefficient of determination R² = 99.6%.

stationary, *i.e.* with zero growth. Carneiro and Hilse (*1966*) and Barringer (*1966*) have assumed that a reasonable estimate of growth rate in the Neolithic would be as high as 0.12% and 0.25% per year respectively. Hassan and Sengel (*1973*) have estimated that the average annual growth rate during the Neolithic was about 0.1%. They suspected, however, that growth rate would be uniform and it could, in fact, attain values of 0.5–1.0% in a period of rapid population increase. Van Bakel (*1981*) has given a growth rate of 0.4 to 0.7% per annum for the period of Neolithization, and similar values have been suggested by Polgar (*1972*). Bandy (*2001*) has calculated that the Neolithic population of the Basin of Mexico in the Formative period grew at approximately 0.74% per annum, and assumes that such a value is a very high rate for an agricultural population with no access to antibiotics or modern medicine. Neustupný (*1983*) have assumed that a growth rate greater than 1% per annum for the Earliest LBK is highly unlike-

ly. Although some authors have shown that a human population could have grown at a rate of around 3% in the past (*Birdsell 1957*), others have argued that the development of agriculture negatively affected human health, led to poorer nutrition, and that higher population density increased the probability of transmission of infectious disease from livestock to humans (*Gage 2005*).

Similar results were obtained in the analysis of total fertility rate, which is the final parameter of the demographic model. TFR vary approximately from 6 to 13 children (Tab. 2). Slightly more than 92% simulations gave estimates of TFR greater than the maximum level of fertility observed in the horticulture populations (Tab. 2). Thus, it is more likely, that LBK fertility was not high enough to allow farmers to spread over Central Europe without admixture with local foragers. Our demographic simulations thus provide a strong argument against the hypothesis of colonization.

Moreover, in our demographic projection, we assume that LBK population enjoyed the most favorable conditions for population growth, because the exponential function (Fig. 2) describes growth that is unbounded by any factor. However, under more realistic conditions, population growth is limited by the carrying capacity of the environment, and the growth rate gradually decreases to zero. Furthermore, we have presumed that stable and maximum rate of growth was maintained during the entire transition period and in the entire area settled at the time. However, several authors argue that popula-
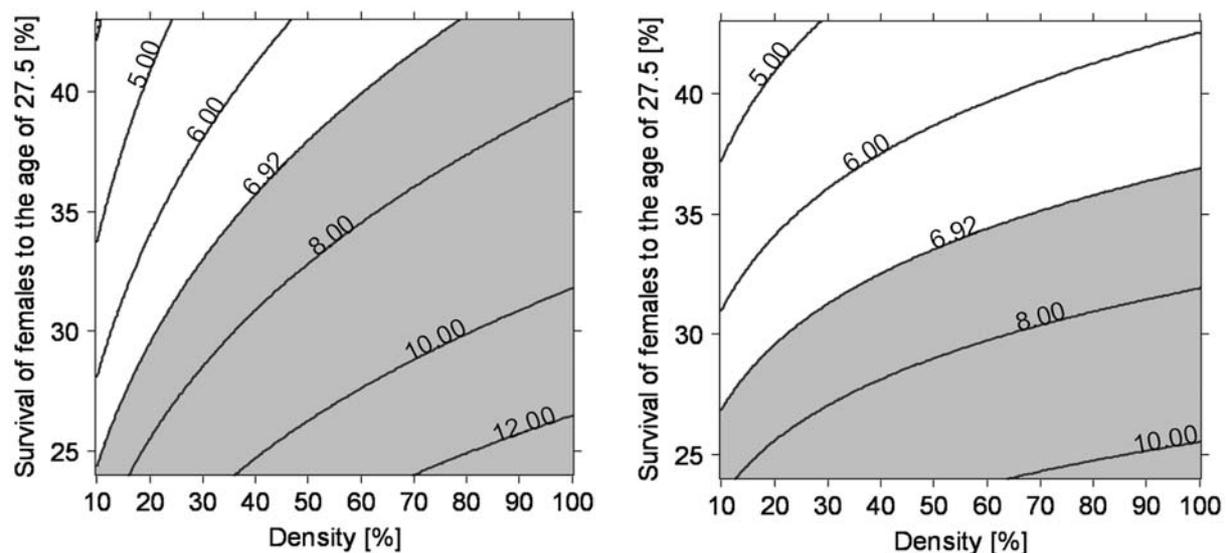

Fig. 7. Contour graphs of the relationship among TFR (displayed as isolines), density ratio, and survival of females for two temporal scenarios of the Earliest LBK expansion. For an explanation of the figures, see text.

tion increase occurred only at the wave front, *i.e.* in the relatively small contact zone between the expanding farmers and indigenous foragers. In the area remaining, which is located behind the front, population growth slows down (*van Andel and Runnels 1995; Pinhasi 2003*). Therefore, the actual level of LBK fertility would have to be greater than we estimated in the simulations. Thus, the colonization hypothesis may be rejected with greater confidence.

The reliability of results of any demographic simulation is directly dependent on the reliability of input parameters. Thus, our motivation was to use only sufficiently reliable parameters. Two of these (generation length and proportion of females at birth) are assumed to be very stable across human populations with natural reproduction (*Hammel 1996*). There is no reason to speculate that they attained different values in the population of LBK farmers. The duration of the spread of LBK has been estimated by numerous independent analyses of radiocarbon data. There is a general agreement among scholars that LBK spread from Transdanubia to the Rhine River during 100–200 years. To achieve satisfactory confidence of the survival of females, we collected a large numbers of estimates (1000) gathered from model life tables with widely ranging mortality levels. On the other hand, the size of the origin and settled area respectively we consider to be the input parameters most prone to bias. Fortunately, the analysis of the effect of the input parameters has revealed (Tab. 3) that the sizes of the origin and settled area have relatively low impact on the results of simulations.

Although the majority of simulations gave unrealistically high estimates of TFR for the LBK population, approximately 8% of them were concordant with the hypothesis of colonization. The demographic conditions of colonization can be inferred from the contour graphs in Figure 7. First, we suppose that population density was maintained at a constant level during the expansion. That is to say, that the population density after LBK expansion was as high as the density in the origin area in Transdanubia. Previously, this assumption would have seemed unlikely, because population pressure was traditionally viewed as the main trigger for the spread of the Neolithic (*Childe 1925*). However, recent authors agree that there is no solid evidence for population pressure in Transdanubia that would encourage the first farmers to migrate (*Willis et al. 1998; Pavúk 2004*), and that even Transdanubia was sparsely populated by people of the Earliest LBK (*Whittle 1996*).

Therefore, a density value of 100% might be a reasonable assumption in the simulations. It can be seen in Figure 7 that there are some TFR estimates below the threshold value of 6.92 children at the density level of 100%. However, they can be found only in simulations where the duration of spread was fixed at 200 years (right contour graph), and where approximately 37% or more females survive to the mean age at childbearing. In contrast, if the spread of the LBK took place within 100 years (left contour graph) it may be ruled out that it was the consequence only of the migratory activity of farmers originating in Transdanubia, because all TFR estimates at the 100% density level are greater than the critical value of fertility.

Another important interpretation may be derived from Figure 7. If we want to obtain acceptable estimates of TFR (white parts of contour graphs), we would have to assume that the population density of farmers who spread from Transdanubia decreased during the transition. To maintain the overall population density in the settled area at 100%, a contribution from local foragers to the establishment of farming communities would have been necessary. What the admixture proportion was is a matter of debate. If we assume the modal level of female survival (around 33%), then the proportion might be 10–30% of farmers to 90–70% of foragers if LBK expanded during 100 years, or 10–50% of farmers to 90–50% of foragers if LBK expanded during 200 years. Such values of admixture proportion correspond well to the results of genetic analyses that have also implied a minor overall contribution from Transdanubian farmers. Studies based on mtDNA have suggested that the contribution of farmers was between 13–20% (*Richards and Macaulay 2000*). According to Y-chromosome evidence, the genetic contribution of Neolithic people may be as low as 22% (*Semino et al. 2000*).

In our model, it is a priori assumed that the age and sex structure of both admixing populations (immigrating foragers and expanding farmers) was identical. However, from the purely demographic view, a fertility level is dependent only on the proportion of females, not males. To keep the overall fertility level of LBK population below the critical value of 6.92 children, immigration from forager communities could have been sex-specific and limited only to females. This consequence inferred from the demographic model is well supported by other evidence. Bentley (*2007*), based on strontium isotope analysis of tooth enamel, has shown that female skeletons were

more common among non-locals in LBK cemeteries. Similarly, Pavlů (*2004*) interpreted a minimum quantity of decorated fineware in Earliest LBK pottery assemblages in Bohemia as the result of the lack of potters' – hunter-gatherer women's – experience. It is argued that females could have joined farming communities through marriage, as has been shown in ethnographic examples (*Kelly 1995*).

Although our demographic simulations clearly support an integrationist view of the Neolithic transition in Central Europe, the model alone does not provide a basis for a more detailed evaluation of an exact mechanism of the process. Several mechanisms which were summarized by Zvelebil (*2000*), *i.e.* demic diffusion, elite dominance, infiltration, leapfrog colonization, and frontier mobility, are possible. To distinguish among these alternatives, restricting ourselves to demographic modeling, several more parameters would enter the model. However, as we have argued above, we preferred to keep the model robust and reliable rather than to speculate with many unreliable parameters.

Conclusion

In this paper we try to show that demographic simulations might be another independent line of evidence in the study of the spread of agriculture in Central Europe. We have demonstrated that the hypothesis of colonization proposed as the mechanism of Neolithic transition in Central Europe may be rejected in 92% of simulations. Colonization would have been possible only if (1) the LBK population was growing in the whole area throughout the transition; (2) the mortality of LBK females was low; and (3) the transition lasted at least 200 years. We have argued that according to ethnographic, demographic, and radiocarbon evidence, these assumptions are unlikely. To allow the farmers to spread over Central Europe, the population density of Transdanubian farmers would have had to decrease. We have suggested that in order to restore the original population density in western Hungary, the contribution of local foragers to the establishment of the Earliest LBK communities would have been necessary. The admixture proportion we have roughly estimated to 10–50% of Transdanubian farmers to 90–50% of local foragers.

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