Modeling Neolithic Dispersal in Central Europe: Demographic Implications

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ABSTRACT On the basis of new examination of ancient DNA and craniometric analyses, Neolithic dispersal in Central Europe has been recently explained as reflecting colonization or at least a major influx of near eastern farmers. Given the fact that Neolithic dispersal in Central Europe was very rapid and extended into a large area, colonization would have to be associated with high population growth and fertility rates of an expanding Neolithic population. We built three demographic models to test whether the growth and fertility rates of Neolithic farmers were high enough to allow them to colonize Central Europe without admixture with foragers. The principle of the models is based on stochastic population projections. Our results demonstrate that colonization is an unlikely explanation for the Neolithic dispersal in Central Europe, as the majority of fertility and growth rate estimates obtained in all three models are higher than levels expected in the early Neolithic population. On the basis of our models, we derived that colonization would be possible only if (1) more than 37% of women survived to mean age at childbearing, (2) Neolithic expansion in Central Europe lasted more than 150 years, and (3) the population of farmers grew in the entire settled area. These settings, however, represent very favorable demographic conditions that seem unlikely given current archaeological and demographic evidence. Therefore, our results support the view that Neolithic dispersal in Central Europe involved admixture of expanding farmers with local foragers. We estimate that the admixture contribution from foragers may have been between 55% and 72%. Am J Phys Anthropol 146:104–115, 2011.

Central European Neolithic transition has been subject to intense debate for more than a century (Gronenborn, 2007). Disagreements prevail about the relative contributions of farmers and hunter-gatherers to the establishment of farming communities. The Neolithic transition in Central Europe had been traditionally explained as representing colonization by farmers of the Linear Pottery Culture (LBK). It was believed that the LBK farmers spread within the 100–200 years between 5600 and 5400 calBC from their area of origin in western Hungary up to the Rhine River in Germany (see Fig. 1) and replaced the population of local foragers (Childe, 1925; Lüning, 1988; Bogucki, 2001). The main argument for colonization in Central Europe was a high speed of LBK dispersal (Robb and Miracle, 2007) that approaches the rate of 6 km per year (Dolukhanov et al., 2005).

The idea of colonization in Central Europe was later criticized by many studies. Subsequent authors provided evidence for continuity between the Mesolithic and Neolithic and accepted that Mesolithic foragers played an active role during the Neolithic transition in Central Europe. That continuity was observed in stone tool production (Gronenborn, 1998; Kind, 1998), hunting activities (Gronenborn, 1999), and reliance on animal protein (Dürrwächter et al., 2006). A significant contribution from Mesolithic foragers to the Neolithic population of Central Europe was also documented by strontium isotope analyses (Price et al., 2001; Bentley, 2007) and genetic analyses (Ammerman and Cavalli-Sforza, 1984; Cavalli-Sforza et al., 1994; Richards et al., 2000; Haak et al., 2005; Palanichamy et al., 2010). As a result, the majority of scholars concerned with the Early Neolithic in Central Europe have abandoned the colonization explanation and accepted that the Mesolithic population was actively involved in the transition (Gronenborn, 2007).

The established consensus among Central European scholars has been recently brought into question by genetic and craniometric analyses. Both lines of evidence again invoked the idea of colonization or at least a major population influx into Central Europe. Bramanti et al. (2009) and Haak et al. (2010) compared mtDNA extracted from late European forager and LBK farmer skeletons and found large genetic differences between the two groups. On the basis of a large craniometric dataset, Pinhasi (2003, 2004) as well as von Cramon-Taubadel and Pinhasi (2011) demonstrated morphological discontinuity

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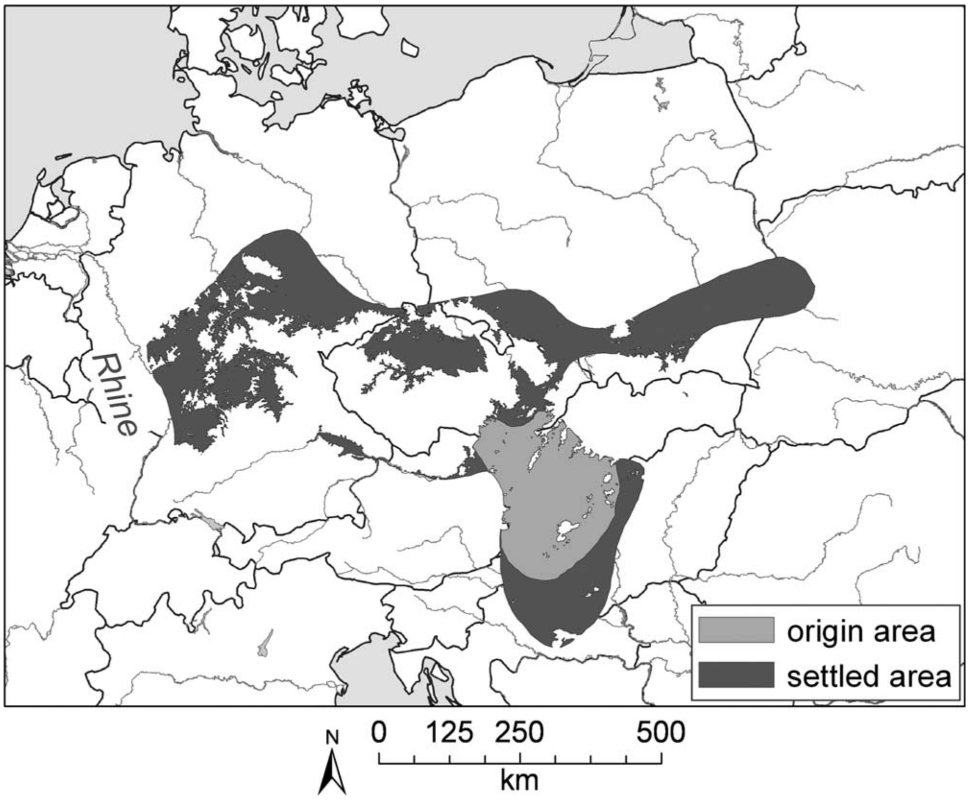

Fig. 1. Map showing area settled by LBK at beginning of dispersal (origin area) and end of dispersal (settled area). Base map adapted from Zvelebil (2004, Figure 7.2) and restricted to area up to 350 m a.s.l. Settled area corresponds to the initial LBK expansion from Hungary up to the Rhine river between 5600 and 5400 calBC.

between Mesolithic foragers and LBK farmers while observing close craniometric affinities between LBK groups and first farmers from Anatolia, Levant, and Greece. Those authors argued that the first farmers of Central Europe immigrated from outside the region and at least initially did not mix with the local female foragers. A significant population influx of farmers was also inferred from observations of the frequency clines for Y-chromosomal markers (Rosser et al., 2000; Chikhi et al., 2002; Semino et al., 2004; Balaresque et al., 2010) and autosomal DNA markers (Dupanloup et al., 2004; Belle et al., 2006) in the modern European gene pool (but see Currat and Excoffier, 2005; François et al., 2010; Morelli et al., 2010; Deguilloux et al., 2011; Myres et al., 2011).

Given the fact that archeological and recent genetic and craniometric evidences provide contradictory views on the existence of colonization in Central Europe, it is appealing to take advantage of alternative approaches. Significant progress has been made recently in demographic modeling of Neolithic dispersal in Europe. The authors modeled the demographic consequences of the Neolithic dispersal on spatial genetic diversity in the modern population of Europe (Currat and Excoffier, 2005; Currat et al., 2008; Ray and Excoffier, 2009; François et al., 2010). Still other approaches to demographic modeling of Neolithic transition in Europe stemmed from population projection methods (Petrasch, 2001) and from hierarchical scale models (Zimmermann et al., 2009). The majority of mathematical models concerned with predicting of the Neolithic front speed in Europe are based on the reaction-diffusion equation originally proposed by Fisher (1937) and applied to the Neolithic dispersal in Europe by Ammerman and Cavalli-Sforza (1973, 1984). The basic reaction-diffusion equation has recently been generalized in many aspects (for detailed review, see Fort and Pujol, 2008; Fort, 2009; Steele, 2009). Several authors have modeled the effect of single-time delay (Fort and Mendéz, 1999; Pinhasi et al., 2005; Isern and Fort, 2009) and multi-time delay (Fort et al., 2004) between individual birth and dispersal; the effect of anisotropic diffusion (Davison et al., 2006; Ackland et al., 2007; Isern and Fort, 2010); age-dependent mortality, fertility and dispersal persistence (Pérez-Losada and Fort, 2010); discrete and continuous dispersion kernel (Isern et al., 2008); the effect of cohabitation of parents and their children (Isern et al., 2008); cultural hitchhiking of neutral traits (Ackland et al., 2007); and the effect of interaction between foragers and farmers (Aoki et al., 1996; Ackland et al., 2007; Fedotov et al., 2008; Fort et al., 2008; Isern and Fort, 2010).

Recent work on mathematical modeling of the Neolithic dispersal in Europe has improved our understanding of the underlying demographic processes. The majority of models were, however, used exclusively at the continental level. Although some of them may have implications at the regional level (Davison et al., 2006; Fort et al., 2008), they are considered as large-scale approximations of locally diverse processes. On a regional scale, the assumptions of continental-level models may be problematic (Currat and Excoffier, 2005). In the region of Central Europe, LBK spread with a speed almost six times faster than in the continent as a whole (Ammerman and Cavalli-Sforza, 1971; Dolukhanov et al., 2005). Adjusting the continental-level models to fit the specific regional conditions in Central Europe may reduce the explanatory power and predictive utility of those models (Bentley et al., 2009).

Assuming colonization, a high propagation rate of Neolithic dispersal in Central Europe would have to be associated with rapid demographic growth of the LBK population (Crubézy et al., 2002; Crubézy et al., 2005). A demographic model based on population projections may provide an estimate of such growth rate and bring evidence to the Neolithic dispersal debate in Central Europe that is independent from other studies. Demographic projections have been used to estimate the growth rates at regional level elsewhere, for example in the Bantu population of Africa (van Bakel, 1981), in the Maori precontact population of New Zealand (Brewis et al., 1990), in the population of Classic Maya of the Honduras (Paine et al., 1996), in the Formative population of Mexico, Peru, and Bolivia (Bandy, 2005), and also in the early Neolithic population of Central Europe (Petrasch, 2001). Previous models using demographic projections were deterministic in nature, however, and neglected the variability inherent in input and output parameters. The advanced approach involves stochastic modeling. A stochastic approach enables the inclusion of uncertainty of input parameters, as it provides a probability distribution of model outputs.

Our goal was to test directly the demographic prerequisites of colonization at the regional level of Central Europe using stochastic demographic projections. In particular, we examined whether the growth and fertility rates of LBK farmers were high enough to allow them to colonize Central Europe within 100–200 years without admixture with local Mesolithic foragers. A negative result would rule out colonization, whereas a positive result could be consistent with both colonization and with dispersal mechanisms that consider contribution from the Mesolithic population. In addition to testing the extreme mechanism of the Neolithic dispersal in Central Europe (i.e., colonization), we tried to estimate the most likely admixture proportions between dispersing farmers and local foragers that best match to our models. Our study differs from other contributions in three aspects. First, we modeled the Neolithic dispersal at the regional level of Central Europe independently from other regions of Europe. Second, we took advantage of stochastic modeling. Third, we developed the concept of an active zone to model its affect on population growth.

MATERIALS AND METHODS

Demographic models for Neolithic dispersal in Central Europe

We produced three stochastic models to simulate growth and fertility rates of the LBK population during its colonization of Central Europe. The data for input parameters were derived from human demography, archaeology, and ethnography. Output parameters were total fertility rate (TFR) and growth rate (r) of the LBK population as would be required by colonization in Central Europe. The principle of all three models is based on methods of population projections (Hinde, 1998). The three models differ only in the size of the area where the LBK population experienced non-zero growth. In Model 1, it is assumed that the LBK population grew across the entire area settled at the time, whereas in Models 2 and 3, the LBK population increased only at the advancing neolithization front (active zone) and was stationary in the rest of the area. Modeling the effect from the existence of an active zone on the LBK growth rate provides an advance over the previous models based on population projections (e.g., Petrasch, 2001). Schematic representations of Models 1–3 are shown in Figure 2.

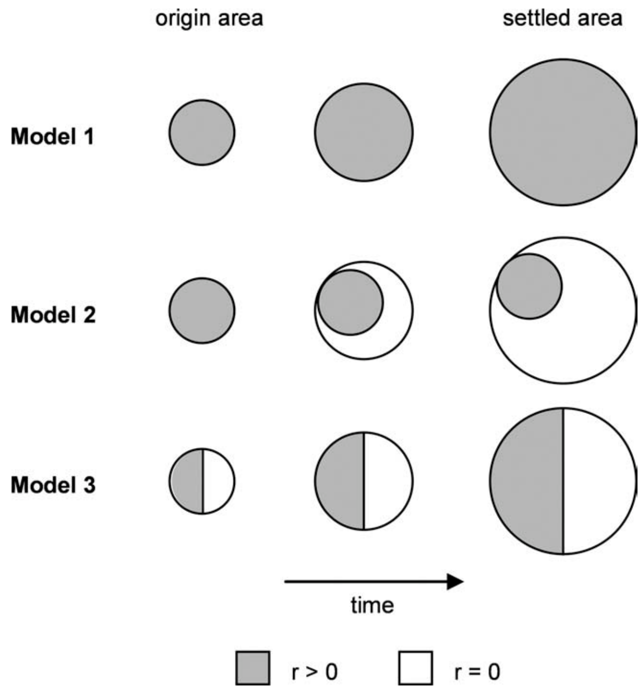

Fig. 2. Schematic representation of Models 1–3. Gray denotes area with positive growth rate ($r > 0$), and white corresponds to areas where LBK population was stationary ($r = 0$). In Model 1, population grows across the entire area. In Models 2 and 3, population growth is limited to the active zone with constant absolute and constant relative size, respectively.

Model 1 (LBK population growing across the entire area). Model 1 proposes a mathematical projection of LBK total population that is derived from the basic equation of exponential growth $P_t = P_0 e^{rt}$ (Hinde, 1998, 201), where P_0 and P_t are the LBK population size at the beginning (P_0) and end (P_t) of its dispersal in Central Europe, t is the duration of dispersal in years, and r is the growth rate of the LBK population which would be required by colonization. Model 1 makes two assumptions: (1) a constant growth rate and (2) no immigration from or emigration to other populations.

The basic exponential equation is further rearranged to produce the growth rate $r = \ln(P_t/P_0)/t$. Because we are not able to estimate LBK population size with sufficient accuracy, we replaced it by the product of area size and population density. The equation is rewritten as $r = \ln(A_t \cdot d/A_0)/t$, where A_0 is the size of the origin area (area occupied by the LBK population at the beginning of the dispersal), A_t is the size of the settled area (area occupied at the end of the LBK dispersal), and d is the density ratio defined as the ratio of population density at the end (d_t) and density at the beginning (d_0) of the LBK dispersal ($d = d_t/d_0$).

Finally, the estimate of r is used to obtain the TFR (average number of children born per woman during her childbearing period). This was achieved by linking both r and TFR to net reproduction rate (NRR). NRR is a measure of population growth and determines the size of the next generation relative to the size of the present gener-

TABLE 1. Input parameters with values used in Models 1–3[a]

Symbol	Description	Min	Max
A_0	Size of origin area (km^2)[b]	32,714	51,446
A_t	Size of settled area (km^2)[b,c]	178,136	232,445
A^A	Absolute size of active zone (km^2)[b]	32,714	51,446
k	Relative size of active zone	0.5	0.9
t	Duration of dispersal (years)	100	200
l_g	Survival of women[d]	0.24	0.43
g	Mean age at childbearing (years)	27.5	
S	Proportion of females at birth	0.4878	
d	Density ratio[e]	1.0	

[a] Absolute size of the active zone is used only in Model 2; relative size of the active zone is used only in Model 3.
[b] Area up to 350 m a.s.l.
[c] Settled area corresponds to the area settled during the initial LBK expansion from western Hungary up to the Rhine River in Germany between 5600 and 5400 calBC.
[d] Proportion of women who survived to the mean age at childbearing. Optimal value of survival is represented by the average value of 0.33 (i.e., 33%).
[e] Ratio of population density at the end of the LBK dispersal (i.e., in settled area) and the population density at the beginning of the LBK dispersal (i.e., in origin area).

ation: NRR = $e^{r \cdot g}$ (Hinde, 1998, 157), where g is mean age at childbearing. Alternatively, NRR can be viewed as TFR adjusted for female mortality during childbearing and the proportion of newborns that are girls: NRR $\cong$ TFR$\cdot S \cdot l_g$ (Hinde, 1998, 186–187), where S refers to the proportion of female births and l_g to the probability that a newborn girl will survive to the mean age at childbearing. Substituting for NRR in the latter equation from the former equation and solving for TFR yields the formula TFR = $e^{r \cdot g}/(S \cdot l_g)$.

Model 2 (LBK population growing in active zone of constant absolute size). Model 2 represents a modification of the projection described in Model 1. In particular, it is supposed that LBK population growth was limited to the active zone situated at the advancing Neolithization front. In the area behind the active zone, population growth had slowed to zero. Such a pattern of expansion and growth is considered to be typical for comparable colonization events, such as Neolithic colonization of Greece (van Andel and Runnels, 1995), expansion of Bantu speakers in Sub-Saharan Africa (van Bakel, 1981), or peopling of the Americas (Fix, 2002).

Model 2 assumes that the total population of the active zone (P^A) was constant during LBK dispersal. Each year, the population of the active zone, which was growing at a rate $r > 0$, increased to $P^A \cdot e^r$ persons. At the same time, the population increment of $P^A \cdot (e^r - 1)$ farmers was expanding to new areas while leaving the population of the active zone constant in absolute numbers. At the end of the dispersal, LBK total population (P_t) consisted of P_0 farmers that were living at the beginning of the dispersal and those farmers that were born in the active zone during t years of expansion: $P_t = P_0 + t \cdot P^A(e^r - 1)$. Substituting the population size by the product of area size and population density and solving for r, the equation becomes $r = \ln\left[\left(A_t \cdot d_t/d^A - A_0 \cdot d_0/d^A\right)/\left(A^A \cdot t\right) + 1\right]$, where A_t and A_0 have the same meaning as in Model 1, and A^A is the size of the active zone. Given the assumption that the population density in the active zone (d^A) was constant and was equal to the density at the beginning of the LBK dispersal (d_0), the formula reduces to $r = \ln\left[\left(A_t \cdot d - A_0\right)/\left(A^A \cdot t\right) + 1\right]$, where d is the density ratio (see Model 1). TFR was computed in the same manner as in Model 1, i.e., TFR = $e^{r \cdot g}/(S \cdot l_g)$, where r refers to the growth rate estimated in Model 2.

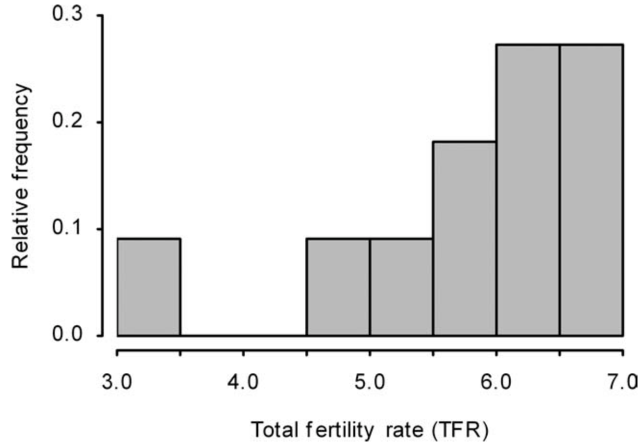

Fig. 3. Total fertility rate (TFR) in the comparative sample (n = 11 horticultural societies).

Model 3 (LBK population growing in active zone of constant relative size). In Model 3, the LBK population grew only in the active zone. Contrary to Model 2, the active zone had a constant relative size (k) with regard to the entire area settled during the dispersal, i.e., $P^A = k \cdot P$. Keeping the relative population size of the active zone constant implies that its absolute size increased during the LBK dispersal. If the population of the active zone grew exponentially, its population increment was $P^A(e^r - 1)$ or $k \cdot P(e^r - 1)$ per year. After t years of LBK dispersal, the total population (P_t) was equal to the sum of the LBK population at the beginning of dispersal (P_0) and the population that resulted from the growth in the active zone: $P_t = P_0 \cdot [1 + k \cdot (e^r - 1)]^t$. If the active zone covers the entire area (i.e., $k = 1$), then Model 3 is equivalent to Model 1, and the last equation reduces to the basic exponential equation $P_t = P_0 \cdot e^{r \cdot t}$. Similarly, to Model 1, substituting population size by the product of the area size and population density and solving for the growth rate gives $r = \ln[((A_t \cdot d/A_0)^{1/t} - 1)/k + 1]$, where A_t, A_0, and d have the same meanings as in Model 1. Finally, TFR is computed identically to Model 1: TFR = $e^{r \cdot g}/(S \cdot l_g)$.

Input parameters

Input parameters are summarized in Table 1. The values were obtained from archaeological, ethnographic, and demographic literature. The size of the origin area (A_0) was derived from maps of the earliest LBK settlement distribution (Kalicz, 1993, Fig. 14, 115; Zvelebil, 2000, Fig. 7.2, 62; Petrasch, 2001, Fig. 2, 16; Bánffy, 2004, Fig. 2, 50) and restricted to the altitudes below 350 m a.s.l. using GIS software (see Fig. 1). The altitude of 350 m a.s.l. is regarded as the upper limit of LBK settlement activity (Rulf, 1983; Pavlů and Vokolek, 1992). Only a small proportion of LBK sites have been discovered at altitudes above 350 m a.s.l. For example, these proportions are 10% in Austria (Lenneis, 2001) and 9% in the eastern part of the Czech Republic (Končelová, 2005). The size of the settled area (A_t) was derived from maps summarizing the distribution of the earliest LBK settlements at the end of the initial stage of its dispersal (Lüning et al., 1989, Fig. 1, 356; Gronenborn, 1998, Fig. 3, 196; Bogucki, 2000, 8.1, 198; Jochim, 2000, 7.3, 187; Zvelebil, 2000, Fig. 7.2, 62). The size of the settled area was estimated using the same procedure as that for the size of the origin area.

The absolute size of the active zone (A^A) was set to the same value as the size of the origin area (i.e., $A^A = A_0$). With this setting, the absolute size of the active zone had attained its maximum theoretical value, because at the very beginning of the LBK expansion, the active zone could not have been larger than the origin area. The relative size of the active zone (k) is constrained by the interval 0.5–0.9, i.e., it is assumed that the LBK population growth occurred in an area that covered from 50% to 90% of the total area settled at the time. Preliminary simulations of Model 3 showed that values lower than 0.5 did not give meaningful values for the output parameter, and input values greater than 0.9 produced results that were comparable to the results from Model 1.

The duration of dispersal (t) was set between 100 and 200 years based on radiocarbon data for the earliest LBK in Central Europe. The interval 100–200 years is generally accepted by scholars, although the absolute data differ from author to author. For example, Price et al. (2001) dated the earliest LBK expansion between 5700 and 5500 calBC, Gronenborn (1999) between 5600 and 5400 calBC, Bickle and Hofmann (2007) between 5600 and 5500 calBC, Gronenborn (2003) between 5500 and 5400 calBC, and Zvelebil (2004) not until between 5400 and 5200 calBC.

The survival of women (l_g, i.e., the proportion of women who survived to the mean age at childbearing) is estimated between 0.24 and 0.43. The optimal value of survival of women for the LBK population is defined here as the mean of the estimated values (0.33). The survival is derived from 7000 model life tables with life expectancy at birth between 18 and 25 years. The interval 18–25 years is the assumed level of mortality experienced by prehistoric populations (Hinde, 2002; Gage, 2005). The sample of 7000 model life tables was created using the four-parameter system described by Ewbank et al. (1983). The method is based on a generic survival function (Ewbank et al., 1983, Table 3, 112), which was transformed by varying each of the four parameters (Ewbank et al., 1983, Fig. 2, 108) into a new survival curve, i.e., to a new life table.

The proportion of females at birth (S) was set to 0.4878 (100 females per 105 males) and mean age at childbearing (g) to 27.5 years of age. Both input parameters are assumed to be relatively stable among human populations with natural reproduction (Hinde, 2002). The density ratio (d) is fixed to the value of 1.0 (i.e., 100%). This means that population density at the end of the LBK dispersal was as high as that at the beginning of the dispersal.

Output parameters

The models' output parameters are total fertility rate (TFR) and growth rate (r). TFR measures the number of children that, on average, had to be born to each LBK woman to allow the LBK population to colonize Central Europe without admixture with other either Mesolithic or Neolithic groups. The growth rate (r) is the intrinsic rate of natural increase that measures the relative change in LBK population size during the colonization in Central Europe.

Comparative sample of TFR and critical TFR

A comparative sample of TFR and critical TFR was created to assess the TFR level of the LBK population obtained in simulations. The comparative sample consisted of 11 cohort TFR estimates of recent horticultural groups ranging from 3.2 to 6.7 children. The distribution is shown in Figure 3. Only horticultural groups were selected because it has been demonstrated (Sellen and Mace, 1999) that subsistence practices are strongly associated with basic demographic parameters in preindustrial populations. Horticulture (extensive agriculture) with cereals and pulses as the main cultivated crops is the preferred subsistence mode assigned to LBK groups (Gregg, 1988).

The comparative sample of TFR was derived from two cross-cultural studies. From the first study (Bentley et al., 1993, Appendix 1, 278), we selected all cohort TFR estimates of horticultural groups with codes 3–6. From the second study (Sellen and Mace, 1997, Table I, 880–881), we collected all estimates of cohort TFR of sedentary extensive agriculturalists with cereals as the main cultivated crop. After TFR of both subsets were pooled, records that differed between the two sources were omitted to achieve reliability.

The critical TFR is estimated at 6.92 children. This value represents the maximum TFR that is assumed to be attained by LBK women during their dispersal in Central Europe. The critical TFR corresponds to the upper limit of a 95% confidence interval for maximum TFR in horticultural societies. The confidence interval was computed from the comparative sample using an unbiased standard bootstrap method (Manly, 2007) with 10,000 iterations and ranged from 6.58 to 6.92 children.

Randomization step

The randomization step represents a stochastic component of the simulations. The randomization step enabled us to take into account the full range of input parameter values (Table 1) and not to reduce its interval estimate to a point estimate (e.g., average value). The principle of the randomization step is described in Figure 4. First, a single value for each input parameter was drawn at random from the intervals specified in Table 1. Fixed values were used for parameters with point estimates. Selected values were substituted into the equations of Models 1–

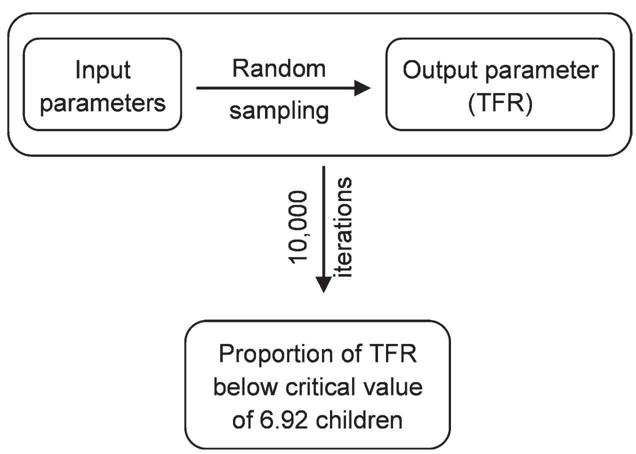

Fig. 4. Stochastic principle of Models 1–3.

3, respectively, and corresponding values were calculated for output variables. Then, a process of random sampling of input parameters and calculation of output variables was run 10,000 times. At the end of the randomization step, 10,000 estimates of r and TFR were obtained. Each of the 10,000 iterations of the model represents one possible demographic scenario for the Neolithic transition in Central Europe. Finally, the proportion of TFR estimates below the critical TFR of 6.92 children per woman was computed. Low values of that proportion indicate that colonization in Central Europe is unlikely because LBK fertility needed for colonization exceeded the fertility potential observed in horticultural societies with natural reproduction.

Statistical treatment

Sensitivity analysis. The relative effect of input parameters on output parameters was assessed using standardized coefficients of multiple regression analysis performed on data obtained from 10,000 iterations of Models 1–3. In the regression model, TFR was used as the dependent variable, and input parameters with interval estimates as independent variables. Those input parameters with point estimates were excluded from the regression analysis, because they have uniform impact on TFR in each iteration. Preliminary analysis of residuals of raw data regression indicated that the relationships between TFR and the input parameters are non-linear. To achieve linearity, the input parameters were transformed by natural logarithm.

Contour graphs. The effects of varying several input parameters on TFR of LBK population were evaluated also graphically by means of contour graphs (e.g., Fig. 5). The contour graphs illustrate the dependence of the LBK TFR on the density ratio (x-axis) and survival of women (y-axis) at three different duration periods for LBK dispersal. The survival of women is shown only for values that may be expected in the LBK population (see Table 1). The remaining input parameters were held constant at their mean values. TFR is represented in the contour graphs by isolines, i.e., lines connecting points of equal TFR value. The white part of the graph corresponds to input parameter combinations that resulted in lower than critical TFR (6.92 children per woman). The gray part represents those values of input parameters that led to TFR estimates above the critical TFR.

The estimates of TFR that are lower than the critical TFR and correspond to a density ratio of 100% represent iterations that support colonization. If no TFR estimate is found under the critical TFR at a 100% density ratio (e.g., left graph in Fig. 5), then colonization is unlikely because the estimated TFR is higher than the expected fertility potential of the LBK population. A density ratio that is lower than 100% indicates admixture of LBK farmers with Mesolithic foragers. This means that estimated fertility of the LBK population was not high enough to maintain constant population density during the dispersal. To meet the assumption of constant population density, the population contribution from a Mesolithic population is needed. The admixture contribution from LBK farmers is estimated as the density ratio that corresponds to critical TFR at the optimal survival rate of 33%. The remaining portion up to a 100% density ratio represents the admixture contribution from Mesolithic foragers.

Simulations were carried out using the MS Visual Basic language (© Microsoft Corporation, 1987–2006) in MS Excel 2003 (© Microsoft Corporation, 1985–2003). Statistical analyses were performed in STATISTICA 6.1 (© StatSoft, 1984–2003). The contour graphs were produced 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).

TABLE 2. Total fertility rate (TFR) and growth rate (r) estimates for Models 1–3[a]

		Median	Min–Max	Proportion of TFR below critical TFR[b]
Model 1	TFR	8.3	5.9–13.0	7.9%
	r (%)	1.1	0.64–1.96	
Model 2	TFR	13.0	7.3–35.8	0.0%
	r (%)	2.6	1.28–5.91	
Model 3	TFR	9.6	6.2–21.6	1.3%
	r (%)	1.6	0.76–3.68	

[a] Values are obtained through 10,000 iterations with density ratio fixed at the value of 1.0 (i.e., 100%).
[b] Critical TFR is 6.92 children per woman.

RESULTS

Model 1

The results for TFR and growth rate (r) for all models are presented in Table 2. The median TFR for Model 1 is 8.3, which is about 1.4 children per woman higher than the expected critical TFR of 6.92. The interval between TFR minimum (5.9) and maximum (13.0) contains the critical TFR, even though the critical TFR is closer to the lower limit of the interval and thus leaves the majority of TFR estimates above the 6.92 children per woman.

TABLE 3. Relative effect of input parameters on total fertility rate (TFR)[a]

			Model 1[b]		Model 2[c]		Model 3[d]	
	Mean	CV (%)[e]	beta	SE_{beta}	beta	SE_{beta}	beta	SE_{beta}
Size of origin area	10.6	1.2	−0.18	0.001	−0.51	0.001	−0.21	0.001
Size of settled area	12.2	0.6	0.10	0.001	0.28	0.001	0.12	0.001
Duration of dispersal	5.0	4.0	−0.46	0.001	−0.64	0.001	−0.53	0.001
Survival of women	−1.1	10.8	−0.87	0.001	−0.49	0.001	−0.68	0.001
Absolute size of active zone	10.6	1.2	n/a	n/a	−0.51	0.001	n/a	n/a
Relative size of active zone	−0.4	45.7	n/a	n/a	n/a	n/a	−0.45	0.001

[a] Results refer to multiple regressions with TFR as dependent variable. Data are log-transformed. All regression models are statistically significant at $P < 10^{-5}$, $n = 10{,}000$.
[b] $R^2 = 0.996$.
[c] $R^2 = 0.981$.
[d] $R^2 = 0.984$.
[e] CV, coefficient of variation; beta, standardized regression coefficients; SE_{beta}, standard error of beta.

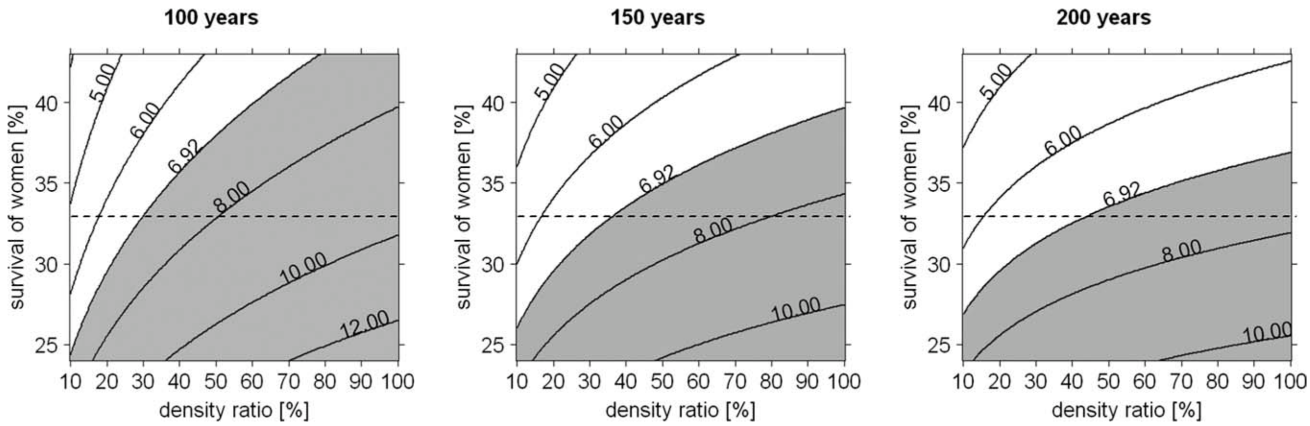

Fig. 5. Contour graphs of simulated TFR in Model 1 for dispersal duration of 100 years (left), 150 years (center), and 200 years (right). For explanation, see Material and Methods.

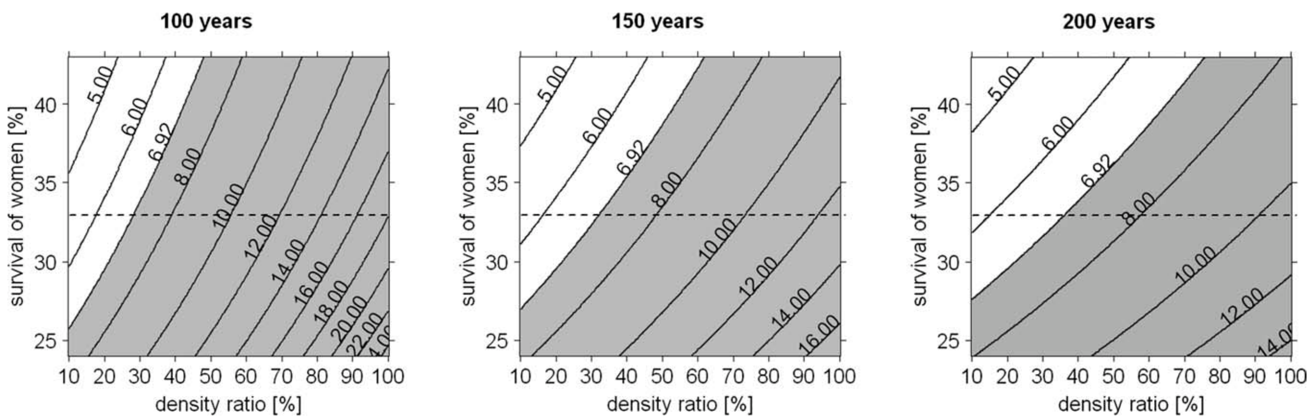

Fig. 6. Contour graphs of simulated TFR in Model 2 for dispersal duration of 100 years (left), 150 years (center), and 200 years (right). For explanation, see Material and Methods.

In 7.9% of iterations, the simulated TFRs lies below the critical TFR of 6.92 children per woman, which means that only the minority of LBK fertility estimates are consistent with colonization. The growth rate estimates are also relatively high for an early Neolithic population, ranging from 0.64% to 1.96% per year.

The results of sensitivity analysis for all models are shown in Table 3. The coefficient of multiple determination for Model 1 ($R^2 = 0.996$) suggests that the regression model provides a good fit to the data. The values of the standardized regression coefficients indicate that the duration of the dispersal (beta = -0.46) and the survival of women (beta = -0.87) have the greatest relative effect on TFR. Both input parameters have a negative effects on TFR, i.e., as duration and survival decrease, the TFR value increases.

The contour graphs for Model 1 are shown in Figure 5. At a dispersal duration of 100 years, none of the TFR estimates is below the critical TFR at the 100% density ratio and within the range of expected values for survival of LBK women (24%–43%). This indicates that, according to Model 1, colonization could not have occurred within 100 years. For 150 years and 100% density ratio, TFR estimates lower than the critical TFR of 6.92 are found only when the survival of women is equal to or higher than 40%. This suggests that, based on Model 1, colonization could not have occurred within 150 years except with a high level of women's survival. Similarly, for 200 years and 100% density ratio, TFR estimates lower than the critical level are found only when the survival is higher than 37%, which means that the colonization in Model 1 is conditioned by survival of women higher than 37%. The survival of women affects also the admixture proportion between LBK farmers and Mesolithic foragers. Assuming the 33% as the optimal survival rate, then for a dispersal period of 100 years, the critical TFR of 6.92 children corresponds to decrease of the LBK density ratio to approximately 30%. The remaining proportion of 70% up to the 100% density ratio level would have been supplied by contribution from a Mesolithic population. For 150 years, the Mesolithic contribution decreased to 65% and for 200 years to 55%.

Model 2

The TFR and r values for Model 2 are summarized in Table 2. None of the TFR estimates is below the critical TFR of 6.92 children per woman. Both TFR and r attain unrealistically large values. The maximum TFR (35.8 children) is a value not observed in human populations. The standardized regression coefficients (Table 3) reveal that the duration of dispersal, the size of the origin area, the absolute size of the active zone, and the survival of women have relatively large effects on TFR in Model 2. The contour graphs for Model 2 are presented in Figure 6. As expected, no TFR estimate is under the critical

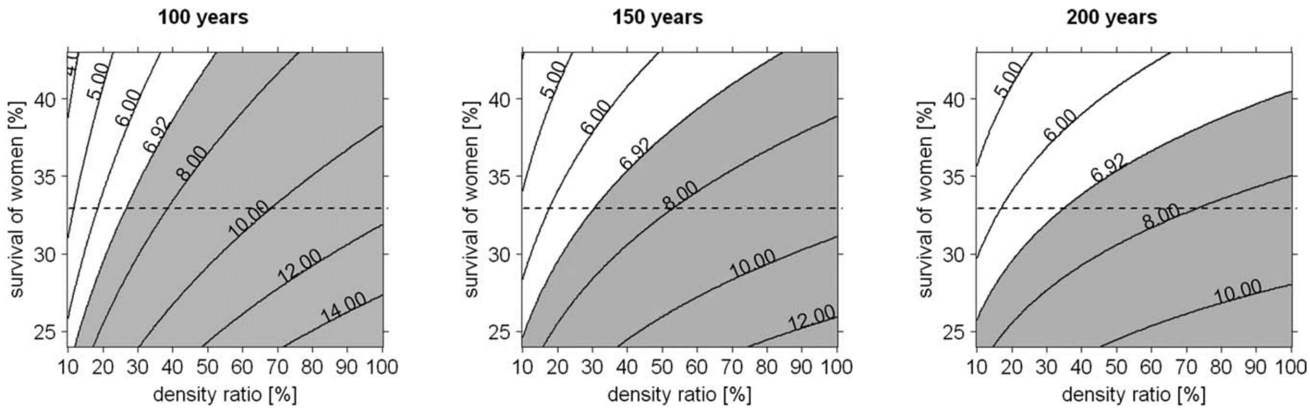

Fig. 7. Contour graphs of simulated TFR in Model 3 for dispersal duration of 100 years (left), 150 years (center), and 200 years (right). Relative size of active zone is set to 0.7. For explanation, see Material and Methods.

TFR of 6.92 children per woman at the 100% density ratio, irrespective of the duration of dispersal. In general, the TFR values below the 6.92 children are associated with low density ratios and/or with high rate of survival of LBK women. At the optimal survival rate (33%), the critical TFR corresponds to density ratios ranging from 28% for 100 years to 35% for 200 years. Thus, the estimated admixture contribution from Mesolithic foragers ranges from 72% to 65%.

Model 3

For Model 3, both TFR and *r* values are intermediate between the values estimated from Models 1 and 2 (Table 2). TFR estimates in Model 3 range from 6.2 to 21.6 children per woman. The lower limit approaches the critical TFR for the LBK population, whereas the upper limit is unrealistically high for any human population. The proportion of TFR values below the critical TFR is low (1.3%), thus demonstrating an inconsistency of Model 3 with colonization in Central Europe. The results of sensitivity analysis for Model 3 show that the survival of women, duration of dispersal, and relative size of the active zone are the input parameters having relatively large effects on TFR (see Table 3). The contour graphs for Model 3 are shown in Figure 7. At the density ratio of 100%, TFR estimates below the critical TFR are found only for duration of 200 years and survival of women higher than approximately 40%. This suggests that Model 3 does not support colonization except for at the longest duration and highest survival rate. At the optimal survival rate (33%), the critical TFR is associated with density ratios ranging from around 28% for 100 years to 35% for 200 years. Thus, the contribution from Mesolithic foragers in Model 3 is estimated at between 72% and 65%, respectively, which figures are similar to the admixture proportion derived from Model 2.

DISCUSSION

The three demographic models presented show weak support for colonization in Central Europe. The strongest support for colonization is provided by Model 1, where 7.9% of iterations satisfy the critical TFR value. However, in Model 1 the colonization is limited to duration of dispersal greater than 150 years and survival of women higher than 37%. Model 2 exhibits the largest discrepancy with the expected demographic conditions of colonization, as no TFR estimate was found below the critical TFR. Model 3 provides results intermediate between Models 1 and 2, where only 1.3% of TFR estimates attained values under the critical threshold of 6.92 children per woman. Thus, Neolithic dispersal in Central Europe seems to be a complex process integrating external immigration and contribution from the local population.

The reliability of simulation results depends on the precision and accuracy of the input parameters. The mean age at childbearing and the proportion of women at birth are the most reliable inputs because these are stable in recent populations having natural reproduction (Hammel, 1996). The reliability of dispersal duration is supported by chronologies built on different samples of Central European radiocarbon dates and produced by different analytical techniques (cf. Gronenborn, 1999; Dolukhanov et al., 2005). The accuracy of women's survival is achieved by using the model life table approach, which enables us to consider a wide range of 7000 mortality patterns that could be expected in the LBK population. The four-parameter system of relational model life tables (Ewbank et al., 1983) provides greater flexibility in modeling the survival of women in comparison with the two-parameter system (Brass, 1971) or with empirical model life tables (e.g., Coale et al., 1983). Moreover, it has an advantage over life tables based on cemetery samples, which are assumed to be unreliable in death rates reconstruction (Sattenspiel and Harpending, 1983; Frankenberg and Konigsberg, 2006). The size of the origin area and size of the settled area are the inputs with potentially low accuracy, which stems from the nature of maps that are produced as generalized representations of the spatial extent of LBK site distribution. However, the results of sensitivity analysis (Table 3) indicate that both the sizes of the origin and settled areas have relatively small effects on TFR in all three models. By contrast, the absolute and relative size of the active zone show strong effects on TFR in Models 2 and 3, respectively, but their reliability cannot be assessed because of the lack of comparable data. To improve the simulations' accuracy, the absolute size of the active zone was set to its maximum theoretical value (i.e., as large as the size of the origin area), and the relative size of the active zone was estimated using the entire interval of realistic values (i.e., 0.5–0.9). Although the values of both input parameters were set to meet the demographic conditions expected for colonization, the outputs of Models 2 and 3 did not support the view that LBK farmers colonized Central Europe without admixture with Mesolithic foragers.

The models presented here are based on an assumption of exponential growth, i.e., growth that is unbounded by any factor. By contrast, human population growth usually follows a logistic pattern, which begins exponentially and then gradually decreases to zero as the population approaches the carrying capacity of the environment (Bentley et al., 2009). We argue, however, that exponential growth serves as a reliable approximation to the logistic growth in the modeling of Neolithic dispersal in Central Europe, as the effect of carrying capacity on the LBK growth was minimal. On an empirical level, Zimmerman et al. (2009) demonstrated, based on their low estimates of LBK population density, that the LBK landscape was not being used to its nutritional carrying capacity. Bogaard (2002, 2004) showed that LBK crop fields were not managed under a shifting cultivation regime, which is associated with frequent relocation due to exceeding carrying capacity. Other authors have argued (Bogucki, 2003; Shennan and Edinborough, 2007; Shennan 2009) that LBK farmers did not compete for resources with local foragers, as the foragers' density was low and foragers settled the areas unsuitable for farming. Moreover, our results show that even when assuming unconstrained growth (i.e., exponential growth), estimated LBK growth and fertility was not sufficient to ensure the demographic requirements of colonization. It is evident that application of growth limited by carrying capacity (i.e., logistic growth) would be even less consistent with the colonization hypothesis.

Colonization is supported in 7.9% of iterations of Model 1, which indicates that this result is marginally insignificant at the conventional 5% level. However, the frequency of iterations that are consistent with colonization is positively associated with the duration of dispersal (cf. Fig. 5). Within the interval of 100–150 years, only 1.0% out of 7.9% of iterations provided TFR below the critical value. Within the interval of 151–200 years, the remaining 6.9% of iterations yielded TFRs estimated below the critical TFR. According to some authors, moreover, LBK dispersal could have been faster than previously assumed, lasting up to 150 years (Dolukhanov et al., 2005) or perhaps only up to 100 years (Gronenborn, 2003). Thus, considering that LBK dispersal took place within less than 150 years, even Model 1 provides TFR estimates that are inconsistent with colonization in Central Europe.

The inconsistency of colonization with the results obtained in Models 1–3 is further demonstrated by the high growth rate (r) estimates (Table 2). The minimum r varies between 0.64% (Model 1) and 1.28% per annum (Model 2), the level higher than the expected demographic potential of the early Neolithic population. It seems that the LBK growth rate did not exceed 1% per annum (Polgar, 1972; van Bakel, 1981; Neustupný, 1983). It is even unlikely that the LBK growth rate exceeded 0.74% per annum, which is considered a very high value for an agricultural population with no access to antibiotics or modern medicine (Bandy, 2005). Although an exceptionally high Neolithic growth rate of 1.24% per annum had been reported by Bocquet-Appel (2002), this value suffers from a large confidence interval of $\pm$1.07%. Reasonable estimates of r in the Neolithic probably are in a range between 0.15% and 0.25% per annum (Barringer, 1966; Hassan and Sengel, 1973). This indicates that the growth rate which would be required by colonization is probably higher than the growth rate reached by the LBK population.

An important assumption in Models 1–3 is constant population density (i.e., $d = 1$, see Table 1), which means that the population densities were equal at the beginning and end of the LBK dispersal. The settlement archaeological record suggests that the population density at the end of the LBK dispersal may have been even 150%–180% higher than at its beginning (i.e., $d = 1.5$–1.8). The settlement density at the beginning of the dispersal is estimated at 0.78 site per 1000 km^2 according to Kalicz, (1993, Fig. 14, 115), and the settlement density at the end of the dispersal is estimated at 1.16 and 1.40 site per 1000 km^2 based on Mazurié de Keroulain (2003) and Petrasch (2001, Fig. 1, 15), respectively. In comparison with the archaeological evidence, the assumption of constant population density represents rather a conservative estimate in our models. Given that the density ratio is between 1.5 and 1.8, our models would lead to even greater inconsistency with colonization in Central Europe as no iteration of Models 1–3 would be found under the critical TFR of 6.92 children per woman.

The results from Models 1–3 suggest that local Mesolithic foragers substantially admixed with expanding LBK farmers. The population contribution from Mesolithic foragers was estimated between 55% and 70% based on Model 1 and between 65% and 72% based on Models 2 and 3. Interestingly, the values are similar in all models and generally correspond to the findings of non-demographic data analyses. Bentley et al. (2002) had examined the strontium isotope ratio in samples from 11 skeletons in an early LBK cemetery at Flomborn and identified seven skeletons of presumably Mesolithic origin. The ratio implies that the Mesolithic contribution may have been around 64%, although the confidence interval is quite large (31%–89% using F distribution).

CONCLUSIONS

The relevance of colonization for the explanation of Neolithic dispersal in Central Europe was examined via stochastic demographic simulations. Three demographic models (Models 1–3) were produced to estimate TFR and growth rate (r) of the LBK population which would have been required by colonization. The results indicate that estimated TFR and r are unrealistically high in comparison to fertility and growth rates expected for early Neolithic populations. Colonization is supported weakly only in Model 1, where realistic estimates of TFR are found with probability of 7.9%. Models 2 and 3 yield results that are even less consistent with colonization. Model 2 produces no realistic TFR estimates, and Model 3 yields realistic TFR estimates with probability of 1.3%. Consequently, colonization does not seem to explain the Neolithic dispersal in Central Europe. Our study supports the view that Neolithic dispersal in Central Europe involved admixture of expanding farmers with local foragers who turned to farming. Moreover, according to our results, expanding LBK farmers might have been demographically in the minority and outnumbered by foragers. We estimate that the contribution from Mesolithic foragers to LBK groups was between 55% and 72%.

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