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Abstract

In this paper I propose that evolutionary demography and associated theory from human behavioral ecology provide a strong basis for explaining the available evidence for the patterns observed in the fi rst agricultural settlement of Europe in the 7th–5th millennium cal. BC, linking together a variety of what have previously been disconnected observations and casting doubt on some long-standing existing models. An outline of relevant aspects of life history theory, which provides the foundation for understanding demography, is followed by a review of large-scale demographic patterns in the early Neolithic, which point to rapid population increase and a process of demic diffusion. More localized socioeconomic and demographic patterns suggesting rapid expansion to local carrying capacities and an associated growth of inequality in the earliest farming communities of central Europe (the Linear Pottery Culture, or LBK) are then outlined and shown to correspond to predictions of spatial population ecology and reproductive skew theory. Existing models of why it took so long for farming to spread to northern and northwest Europe, which explain the spread in terms of the gradual disruption of hunter-gatherer ways of life, are then questioned in light of evidence for population collapse at the end of the LBK. Finally, some broader implications of the study are presented, including the suggestion that the pattern of an initial agricultural boom followed by a bust may be relevant in other parts of the world.

Keywords

evolutionary demography, Neolithic, agricultural spread, Europe, Aldenhovener Platte, Linear Pottery Culture (LBK), demic diffusion, ideal despotic distribution, spatial population ecology, reproductive skew theory.

Cover Page Footnote

Some parts of this paper previously appeared in my paper "The Spread of Farming into Central Europe and Its Consequences: Evolutionary Models," in The Model-Based Archaeology of Socionatural Systems, Timothy A. Kohler and Sander E. van der Leeuw, eds. (Santa Fe, NM: School for Advanced Research, 2007) and are reprinted with permission. Figure 1 is reproduced with permission from R. J. Quinlan, "Human Parental Effort and Environmental Risk," Proc. R. Soc. Biol. Sci. 274:123 (Figure 2) (2007). Figures 2 and 3 are reproduced with the author's permission.

Evolutionary Demography and the Population History of the European Early Neolithic

STEPHEN SHENNAN[1]

Abstract In this paper I propose that evolutionary demography and associated theory from human behavioral ecology provide a strong basis for explaining the available evidence for the patterns observed in the first agricultural settlement of Europe in the 7th–5th millennium cal. BC, linking together a variety of what have previously been disconnected observations and casting doubt on some long-standing existing models. An outline of relevant aspects of life history theory, which provides the foundation for understanding demography, is followed by a review of large-scale demographic patterns in the early Neolithic, which point to rapid population increase and a process of demic diffusion. More localized socioeconomic and demographic patterns suggesting rapid expansion to local carrying capacities and an associated growth of inequality in the earliest farming communities of central Europe (the Linear Pottery Culture, or LBK) are then outlined and shown to correspond to predictions of spatial population ecology and reproductive skew theory. Existing models of why it took so long for farming to spread to northern and northwest Europe, which explain the spread in terms of the gradual disruption of hunter-gatherer ways of life, are then questioned in light of evidence for population collapse at the end of the LBK. Finally, some broader implications of the study are presented, including the suggestion that the pattern of an initial agricultural boom followed by a bust may be relevant in other parts of the world.

The foundations for understanding demographic processes, whether in prehistory or the present, lie in Darwinian evolutionary theory and more specifically in life history theory (Charnov 1993; Hawkes and Paine 2006) and human behavioral ecology (E. A. Smith and Winterhalder 1992; Winterhalder and Smith 2000). It can be assumed that humans, like other animals, have evolved to maximize their reproductive success. The idea that children are a good in themselves, rather than simply a means to an end (e.g., to increase the pool of agricultural labor), seems to

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KEY WORDS: EVOLUTIONARY DEMOGRAPHY, NEOLITHIC, AGRICULTURAL SPREAD, EUROPE, ALDENHOVENER PLATTE, LINEAR POTTERY CULTURE (LBK), DEMIC DIFFUSION, IDEAL DESPOTIC DISTRIBUTION, SPATIAL POPULATION ECOLOGY, REPRODUCTIVE SKEW THEORY.

be held in virtually all human cultures. Decisions to have children or not and how much to invest in them are made at the individual or household level in light of individual interests and the circumstances that affect them. Those circumstances also affect the outcomes of unconscious "decisions," such as changing lactation spans arising from changing activity patterns (Bocquet-Appel 2008). The macroscale population-level results of these decisions are unintended outcomes, not goals of regulation (Voland 1998).

There are trade-offs between the maximum number of children that can be produced and the maximum number that can be brought to the stage of being successful parents themselves, because of the costs of parental investment. Thus, for example, Gillespie et al.'s (2008) analysis of historical demographic data from 18th-century Finland demonstrated that there were diminishing returns in maternal fitness with increasing maternal fecundity for women from landless but not from landowning families. If changed conditions of some kind reduce the severity of those trade-offs, then people will take advantage of them and population will expand to new limits (cf. Wood 1998). Those limits will not in general be set by the starvation carrying capacity but by the point at which external conditions have a density-dependent effect on individual choices relating to fertility, survival, and parental investment, such that mean reproductive productivity and mean survival balance one another (Puleston and Tuljapurkar 2008; Sutherland 1996: 108–113). Those changed conditions may be entirely exogenous. For example, M. A. Smith and Ross (2008) suggested that an increased intensity of human occupation in central Australia about 1,500 years ago was associated with the spread of summer-rainfall grassland and increased rainfall. They may also stem from cultural innovations. Thus Gibson and Mace (2006) showed that the installation of water taps in an Ethiopian village led to increased fertility as a result of the reduced energy load for women arising from not having to carry water long distances, and Kramer and McMillan (2006) found a similar result with the introduction of a water pump and maize mill in a Maya village.

It follows that any reasonably sustained regional population increase is likely to be an indicator of new conditions that promote increased reproductive success for those who respond appropriately. Population stability, on the other hand, is an indication that a local ceiling has been reached, a process that will not take long given the rapid increases in numbers that even relatively low growth rates produce. Discussions of the demographic consequences of new adaptations, such as cereal- and pulse-based agriculture, often emphasize the higher population growth rates produced. However, on an archaeological time scale the absolute increases in population density that are sustainable are at least as important, if not more so; no growth phase can last long before density-dependent checks arising from physiological factors or economically based decisions about age at first marriage lead to equilibrium population levels. But new adaptations will be especially successful if dispersal opportunities are available to the human populations practicing them (Voland 1998), so that the consequences of the individual reproductive decisions are shifted, and when a local population ceiling has been reached, expansion can continue elsewhere. In the circumstances of range expansions, human populations are “food-limited” rather than “space-limited” (Lee and Tuljapurkar 2008).

Periods of population growth, as Bocquet-Appel (2002), Bocquet-Appel and Naji (2006), and others (e.g., Sattenspiel and Harpending 1983) have shown, result in an increased representation of younger individuals in the population. If we had the burials associated with the expansion of populations out of the late glacial refugia into northern Europe at the end of the last Ice Age, we would probably find essentially the same pattern even if the growth rates were lower. However, three potential features of the expansion of agriculture may make this different in terms of demographic properties, apart from the often discussed effect of sedentism on fertility. First, in many areas the sustainable productivity of agriculture per unit area is so much greater than the possibilities offered by foraging that population increase can continue for longer for a given rate of growth, leading to higher equilibrium densities before density-dependent checks take hold. Second, the amount of parental investment per child required to produce successful adults will probably be higher for foragers than for farmers. Kaplan et al. (2000) showed that for males in particular, it is not until the age of 20 that they start producing more than they consume. In agricultural societies children become productive earlier and older children actually subsidize the investment in younger ones (Boone 2002; Kramer and Boone 2002). Finally, to the extent that dependence on agriculture led to poorer diets and a greater incidence of infectious disease over which parents had little or no control and thus led to increased infant mortality and decreased life expectancy at birth, life history theory predicts a shift in reproductive strategy to producing larger numbers of offspring and investing less in any one of them. In other words, in these circumstances those individuals that switch to this strategy will, on average, have greater reproductive success. The existence of the predicted pattern is shown by Quinlan (2007) and in Figure 1.

In what follows I first look at the evidence for large-scale demographic patterns and what they tell us about the corresponding processes associated with the beginning of the Neolithic and their implications for current models. I then examine the mesoscale of these demographic processes and their social consequences before turning to the factors that delayed the spread of farming into northwest Europe for more than a thousand years after its initial arrival at the Rhine.

The Spread of Farming into Europe: Demic Expansion and Its Consequences

By the end of the 7th millennium cal. BC, groups with agricultural economies had spread through southeast Europe into the Carpathian basin (Biagi et al. 2005). The so-called Linear Pottery Culture (LBK) that characterizes the first farming groups of central Europe appears to have originated in western Hungary and eastern Austria c. 5600–5500 cal. BC. It spread westward extremely quickly. The area covered by the earliest LBK seems to have been settled in less than 150

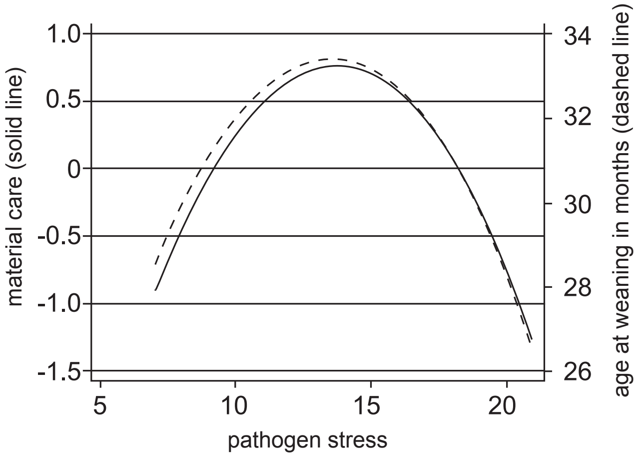

Figure 1. Quadratic associations between pathogen stress and parental effort based on a multiple linear regression analysis of the relationship between environmental risk and parental effort using data from the Standard Cross-Cultural Sample. From Quinlan (2007).

years (Petrasch 2001); subsequently it expanded still further. However, it should be emphasized that these early agricultural occupations were not spatially continuous but restricted to particular patches with favorable conditions for early farming (van Andel and Runnels 1995), and this partly explains the rapidity with which the spread occurred. As the work of Bocquet-Appel (2002) and the radiocarbon date probability distributions discussed later show, the expansion also involved rapid population growth. On the basis of studies of the number, size, and density of settlements of the LBK in central Europe, Petrasch (2001, 2005) has calculated extremely high population growth rates between 0.9% and 2.7% for these first farming societies. Detailed fieldwork in Germany in the western Rhineland has enabled this growth and expansion process to be traced on a local scale (e.g., Zimmermann 2002; see also Dubouloz 2008).

The mechanisms involved in the spread of farming into Europe and specifically the question of whether this occurred as a result of demographic expansion or cultural diffusion have been disputed for many years and are the subject of continuing debate. In my view the evidence increasingly favors the demic diffusion process originally proposed by Ammerman and Cavalli-Sforza (1973) as the primary mechanism for the initial expansion: that the spread of farming into Europe was a classic example of a dispersal opportunity. In large parts of Europe, away from coastal and riverine areas with rich aquatic resources, Mesolithic hunter-gatherer population densities were low. However, the areas with low population densities included zones that were suitable for growing cereal crops and thus could sustain much higher densities of farmers than hunter-gatherers. Moreover, the combination of annual cereals and domestic animals, in addition to supporting higher population densities and therefore greater reproductive success before the new higher ceiling was reached, was extremely portable, far more so than many other agricultural systems. The result was a process of demic diffusion, which would have rapidly subsumed any small hunter-gatherer populations existing in the areas initially occupied by early farmers.

Recent investigations using a variety of proxies for prehistoric population patterns strongly support this argument. The radiocarbon-date-based study by Gamble et al. (2005), which shows population fluctuations in the western half of Europe in the late Paleolithic and Mesolithic, indicates that these hunting and gathering populations were not stable but expanded and contracted, responding to shifting resource opportunities as the climate changed. What is particularly interesting in the present context is that populations in the later Mesolithic (excluding certain coastal and riverine areas) were at historically low levels, presumably because the developing forest cover resulted in decreasing animal population densities.

Figure 2 shows the summed date probabilities approach taken forward into the Neolithic for a number of broad areas where good data are available. In all cases where farming is associated with the appearance of LBK settlements in the second half of the 6th millennium BC (Belgium, Netherlands, Germany), its impact is clearly apparent: Low Mesolithic population levels are succeeded by a massively increased LBK population; equally striking is the indication of a major decline in population at the end of the LBK in the early 5th millennium; this will be considered later.

Niekus (2009) is right to point out that we should always be aware of the many possible biasing factors that might affect the validity of summed radiocarbon probability distributions as population proxies, but the pattern of a decline in population levels over the course of the Mesolithic has also been recently shown at a more detailed level by Vanmontfort's (2008) study of trends in Mesolithic occupation in several areas of the Low Countries on the basis of the chronological and spatial distribution of microliths. It appears that those specific areas of the Low Countries that subsequently became LBK early farming nuclei had long been devoid of Mesolithic occupation. It may be, then, that the incoming LBK farmers deliberately settled in areas that were marginal to already low-density Mesolithic populations (Vanmontfort 2008: 157). Vanmontfort (2008: 158) goes on to reject Gregg's (1988) mutualistic model for forager-farmer interaction, arguing that, to the contrary, either the presence of the LBK resulted in a retreat of foraging populations or hunting-gathering activity simply survived longer further away from them; Vanmontfort also argues that there is no evidence for the hostile forager-farmer relations proposed by Keeley (1992). In general, the evidence for farmer-forager interaction during the LBK in the west (and indeed in many if not most other areas) is remarkably slight.

Similar arguments have been made for a discontinuity or hiatus between the late Mesolithic and early Neolithic in many parts of southeast and Mediterranean Europe, on the basis of gaps in site stratigraphies, especially caves (Berger and Guilaine 2009; Bonsall et al. 2001b).

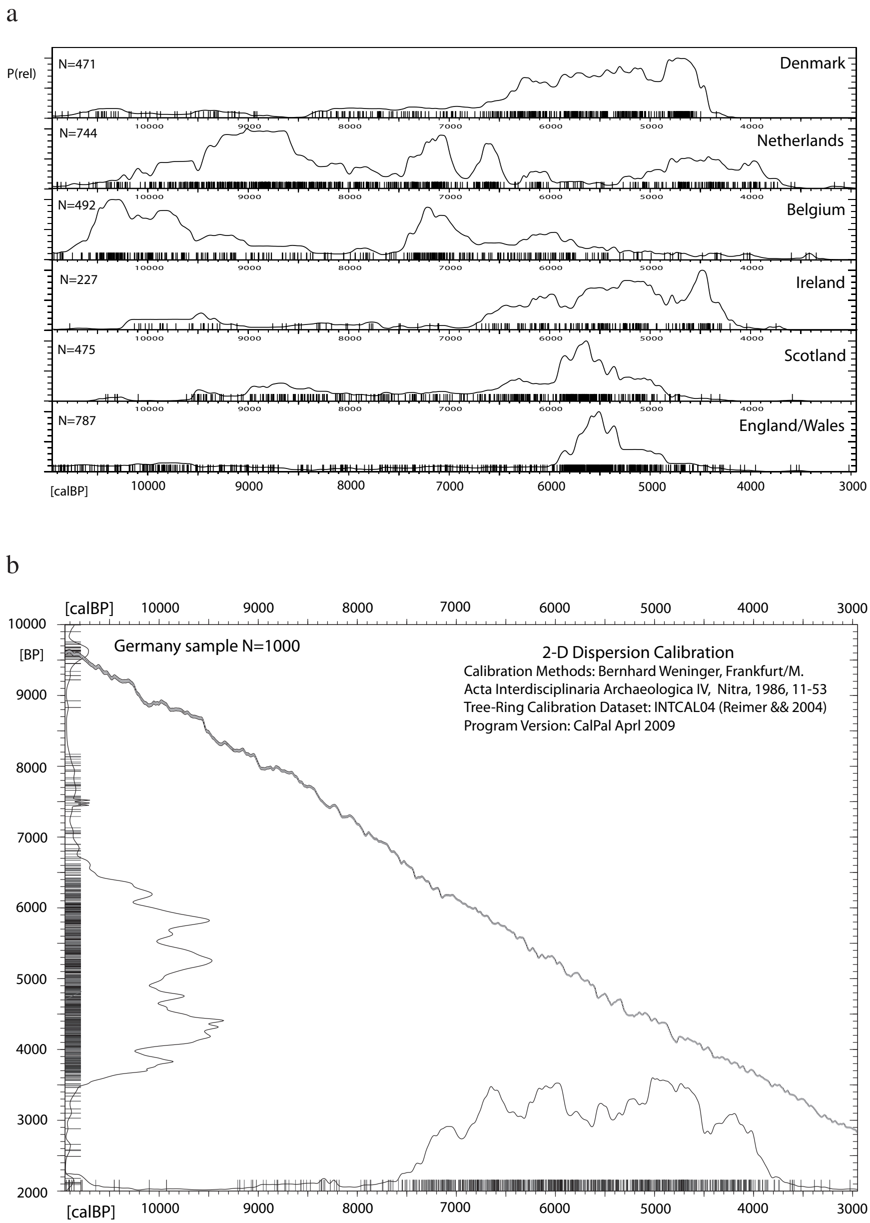

Figure 2. (a) Cumulative calibrated radiocarbon age distributions for selected countries from the Northwest European Mesolithic-Neolithic Database, in the age range 11,000–4,000 cal. BP. From Weninger et al. (n.d.). (b) Cumulative radiocarbon date probabilities for Germany (from Weninger et al., n.d.).

Population Ecology of Demographic Expansion Processes: The Mesoscale

There has been a tendency to assume, not least on the part of opponents of the idea, that demic diffusion was responsible for the spread of farming, that demographic growth models of the spread of farming presuppose that spatial expansion would not have been triggered until local populations were coming close to an absolute local carrying capacity. That this cannot have been the case is suggested by the speed of the expansion into southeast, central, and Mediterranean Europe and is documented by the fact that in certain areas we can see that new places were colonized before others reached any sort of carrying capacity. Therefore it has been suggested that cultural diffusion through existing forager populations is a more convincing mechanism.

The basis for understanding why further expansion does not necessarily presuppose demographic saturation is provided by principles derived from the theory outlined earlier, in this case as they relate to decision making concerning spatial behavior (Sutherland 1996; Winterhalder and Kennett 2006: 16). These principles predict the distribution of individuals in relation to resources on the basis of the ideal free distribution. When individuals (of any species) who are seeking to maximize their probability of survival and reproductive success move into a new area, they will occupy the resource patch that gives them the best returns. In fact, as noted, it has been apparent for a long time that early agricultural occupations were not continuous but restricted to particular patches with favorable conditions for early farming (e.g., van Andel and Runnels 1995). As more individuals occupy the patch, the returns to each individual decline, to the point that the returns to an individual from the best patch are no better than those from the next best patch, which at this point has no occupants. The returns from both patches are then equal, and they will be occupied indiscriminately until the population grows to the point at which there is an equal benefit to be gained from occupying a still worse patch, and the process is repeated.

When there is territoriality, however, the situation is different. Here the so-called ideal despotic distribution applies. The first individual occupying an area is able to select the best territory in the best patch. Subsequent individuals settling there do not affect the first arrival but have to take the next best territory, and so on, until there comes a point at which the next settler will do just as well by taking the best territory in the next best patch. Subsequent individuals will then take territories in either patch where the territories are equally suitable. In contrast to the ideal free distribution, where new settlers decrease the mean return for everybody, including those who arrived first, in an ideal despotic distribution the returns depend on the order of settlement, so that the initial settlers of the best territory in the patch will do best, so long as they can defend the territory against anyone who might seek to take it from them.

It is proposed, then, that for the spread of farming into Europe, the new households being formed as population expanded would have been evaluating the costs and benefits of staying near their parents' household or finding somewhere else, following the principles of the ideal despotic distribution. All that would have been required for further spatial expansion is a shift in the balance of costs and benefits between accepting the next best local territory available and taking the risk of finding and settling a new top quality patch some distance away, allowing for the fact that to be the first occupant of a more distant patch might have some disadvantages, such as limited access to reproductive partners or lack of local support if the crops failed; this is the so-called Allee effect (Sutherland 1996: 10–11). It is this that accounts for the rapid expansion of the LBK, coupled with the fact that some of the move distances for newly formed communities were quite long (cf. Bogucki 2003). For the LBK expansion there may well have been many new locations that were equally satisfactory, or at least we have no evidence in the physical characteristics of the places initially occupied that they were very different from one another, but it is clear that early in the expansion process many new locations were occupied almost simultaneously (Zimmermann 2002).

If we assume that the principles of the ideal despotic distribution hold, we can make some further predictions not just about the initial process of patch colonization but also, perhaps more interestingly, about the subsequent history of patch occupation. First, we expect the founding settlement in a particular area to be the dominant one. This is exactly what we find in areas where detailed work has been done. The site of LW8 in the Merzbachtal in the Aldenhovener Platte region of the western Rhineland, for example, was occupied throughout the approximately 400 years of the local LBK sequence and was always the largest (Lüning and Stehli 1994; see also Dubouloz 2008). Apart from its presumptively good location from the farming point of view, it also seems to have had a special position as a redistribution center for lithic resources obtained from a major source of high-quality raw material some distance away to the west, either as a result of controlling exchange relations with local foragers beyond the agricultural frontier or through direct access to the source (Jeunesse 1997; Zimmermann 2002). Moreover, it was at LW8 that a ditched enclosure of possible ritual significance was constructed in the latest local phases of LBK occupation.

Despite the high population growth rate, initially there would have been no competition between different communities because, as new households were formed, they would have been able to move to favorable locations elsewhere. Relatively rapidly, though, the individual microregions began to fill up and reach an equilibrium population size (Figure 3). This would have led to increased competition between groups and a reduced possibility of leaving a group and setting up a successful independent household in the face of disputes or attempts at exploitation, as adjacent settlement areas would all have been filling up at the same time. Reproductive skew theory (Summers 2006; Vehrencamp 1983) predicts that both increased intergroup competition and reduced colonization opportunities would lead to increased inequality within groups as the available options of subordinate members decreased.

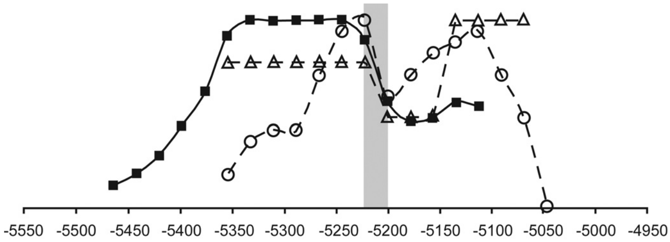

Figure 3. Numbers of houses existing at different times during the Linear Pottery Culture (LBK) period from three LBK sites in Germany; numbers rescaled so that all sites have the same maximum value. From Strien and Gronenborn (2005). Circles, Merzbach; squares, Vaihingen; triangles, Bischoffsheim.

Over time these local LBK societies do indeed seem to have become more unequal. The evidence for this comes from both settlements and cemeteries. For the settlement evidence the case was made by van der Velde (1990), on the basis of sites in the southeastern Netherlands and the Aldenhovener Platte. LBK houses seem to be made up of three modules (northwest, central, and southeastern parts) with different functions. Some houses have only the central part, others a central and northwest element, and others still all three parts. The southeastern part, believed to be the front, is generally argued to have included a granary. Van der Velde proposed that the distinctions between houses with larger and smaller numbers of elements related to the wealth and status of their associated households and could not be explained by changing household composition arising from family life cycles or qualitatively different household compositions (van der Velde 1990). At the Dutch sites the houses with all three elements had more room than the others (the individual house elements were larger), and more stone adzes were associated with them. At the LW8 site cereal processing waste was preferentially associated with the large houses (Bogaard 2004). Elsewhere there is evidence of higher proportions of domestic animal bones being associated with large houses and more remains of hunted animals being associated with smaller houses (Hachem 2000). On the basis of a spatial analysis of the settlements he studied, van der Velde also showed that the units that make up the settlements suggest the existence of long-term social patterns: Particular households and groups of households seem to have continued through time, with continuing inheritance of status witnessed by the rebuilding of houses of the same type in the same places. Moreover, it seems that over time the proportional frequency of small houses, as opposed to large ones, increased, suggesting growing inequality. Coudart's (1998) analysis of LBK houses led her to conclude that major rank or wealth differentiation did not exist, but she too pointed to some indications of status differences. She noted, for example, that granaries were never associated with small houses and that some buildings were more spacious than others. Interestingly, she also suggested that perhaps the largest houses were associated with the groups that had first established the settlement.

As far as burials are concerned, it is clear that there were complex patterns of spatial differentiation involving both burial within settlements and separate cemeteries, mainly of individual inhumations, which are rare in the earliest LBK phases. Jeunesse (1997) concluded that the earliest burials present a picture of relatively egalitarian societies, with indications of achieved status for older men, whereas the later burials tend to have a small group of graves, including child burials, clearly distinguished from the rest by the presence of markedly richer grave goods and possible symbols of power. This is the case, for example, with the cemetery of Niedermerz 3, which belonged to the settlements of the Merzbachtal on the Aldenhovener Platte and which was established in the 52nd century cal. BC. Cemeteries would have come into existence for precisely the reasons proposed in the long-standing Saxe-Goldstein model: to represent an ancestral claim to territory in the face of increasing competition as local carrying capacities began to be reached. Indeed, precisely this argument has been used by van der Velde (1990) and Kneipp (1998) (cited by Zimmermann 2002) to account for the establishment of the Niedermerz cemetery. Increased competition also provides a basis for explaining the deposition of rich grave goods as a form of costly signaling (Bliege Bird and Smith 2005; Neiman 1997), in which the ability to make extravagant displays represents an honest signal of a group's power and control over resources that would otherwise not be apparent. Thus the number of rich burials would not simply be a reflection of the size or power of, for example, a senior lineage but of the competitive pressure it was under in particular places and times.

It is not clear whether the processes described here occurred throughout the LBK distribution, but they certainly seem to have been prevalent in its western half on the basis of the evidence. The reasons for their prevalence seem to be twofold. First, similar processes of demographic growth and local filling up would have been going on everywhere that the LBK settled [see, e.g., Ebersbach and Schade (2004) for another example]. Second, all these local societies ultimately had a common origin and thus a similar starting point in terms of social norms and institutions. This is apparent in the material dimensions for which we have evidence.

Decline and Disappearance of the LBK

The emergence of local inequality in terms of hereditary social and economic distinctions based on priority of access during the colonization process is not the only widespread institutional trend to be observed in the course of the LBK. A pattern of ditched and/or palisaded enclosures in later occupation phases seems to characterize many settlement microregions. Kerig (2003) suggested that the enclosures represent the emergence of a new type of social institution that integrated larger numbers of people into a single social unit. The existence of institutions capable of bringing large numbers of men together for warfare, at least on a temporary basis, is suggested by the scale of both the Talheim and Asparn-Schletz late LBK massacres (Wahl and König 1987; Wild et al. 2004). In the Talheim case the remains of 34 individuals were recovered, and in the Asparn-Schletz case at least 67, even though not all of the enclosure ditch was fully excavated. These figures imply large numbers of attackers.

Whether the LBK enclosures were themselves always defensive constructions is not really the point if one accepts that they represent a new kind of social institution involving larger scale integration. One role of the social institutions associated with the enclosures may have been precisely to overcome the tensions arising from intragroup inequality and to make corporate groups act more effectively as entities, as intergroup competition became increasingly important (cf. Read and LeBlanc 2003). In light of the evidence for massacres, it can be suggested that once institutions emerged that integrated larger numbers of people into a cooperating unit that was competitively successful, other groups had little option but to copy them if they wished to avoid potentially disastrous consequences, even if the global outcome was poorer conditions for all. Growing intergroup hostilities may be behind the breakdown of previously long-standing lithic exchange networks at this time, as well as one of the factors that led to the population crash, or at least decline, in many areas of the western LBK apparent in the aggregate radiocarbon patterns discussed earlier (see Figure 2) but also more locally (e.g., Ebersbach and Schade 2004; Zimmermann 2002). However, the reasons for this decline remain obscure. It is not clear that the violence was on a sufficiently large scale to account for it, and climate-based arguments are not sufficiently clearly specified in terms of their mechanisms and proposed consequences (e.g., Dubouloz 2008; Schmidt et al. 2004).

Hiatus in the Spread of Farming to Northwest Europe

It has long been apparent that the spread of farming from southwest Asia to northwest Europe did not occur at the same rate throughout its extent [see Bocquet-Appel et al. (2009) for an especially clear demonstration of this point]. The contrast between its appearance at the western and northern edges of the central-west European loess zone before 5000 cal. BC and its expansion farther north and northwest into Britain and southern Scandinavia a thousand years later is particularly striking. Since the work of Zvelebil and Rowley-Conwy (1986) and subsequent papers by Zvelebil (e.g., 1996), the standard model of the spread of farming in temperate continental Europe beyond the initial core areas of the Balkans and the loess zone has been the following: an initial period when knowledge of agricultural resources and other aspects of farming material culture were available to local foragers; a substitution phase when foragers interacted increasingly with farmers and their existing lifeways were disrupted, because of such processes as a loss of hunting territories and increasing preferences of women in forager communities to marry farmers; and, finally, the full-scale adoption of farming. It is increasingly clear that this model does not fit the evidence that is becoming available.

Most important, this model implies a steadily growing pressure of farming populations on surviving hunting-gathering groups, especially in frontier areas such as northwest Europe, where the spread of farming halted for a millennium. However, as we have seen, the cumulative date probabilities for Belgium and the Netherlands in Figure 2 point to a steep decline in and not a collapse of farming populations at the end of the LBK. The same occurs in the western Rhineland and elsewhere. Many different lines of evidence support the argument that these areas were largely abandoned and then subsequently reoccupied, or at the least saw substantial population reductions. Whatever the reasons for it, the collapse of the farming, not the forager, populations is the opposite of what the Zvelebil model leads us to expect.

The paradigm case of the availability-substitution model for the adoption of farming is generally taken to be the Ertebølle culture of Denmark and northern Germany, with increasing evidence for contacts with farming groups to the south over the course of the 5th millennium BC, but a glance at the rising cumulative radiocarbon probability curve for this period (Figure 2, Denmark) does not suggest much in the way of disruption; to the contrary, it points to a steadily rising population curve until slightly before 4000 BC, although then there is an indication of a slight dip, and the beginning of the Neolithic at c. 3800 cal. BC does mark a rapid and major dietary shift from aquatic to terrestrial cultivated resources (Fischer et al. 2007). If there was some sort of crisis in the southern Scandinavia foraging system that resulted in a switch to farming, it was played out in an extremely short period of time between c. 4000 and 3800 cal. BC.

In fact, if we look across all the northwest European date curves shown in Figure 2, from several different regions, we see indications of a population increase in the centuries just before or just after 4000 BC. In the British Isles this increase is associated with the initial appearance of agriculture. In the coastal zone of the Low Countries the increase is associated with the adoption of cereal cultivation as one strategy among many by local forager groups (Cappers and Raemaekers 2008; Vanmontfort 2008), with no suggestion that this was precipitated by existing growing local farming populations. As Bonsall et al. (2001a) pointed out a number of years ago, the Zvelebil model has no mechanism to account for this simultaneity, nor indeed to account for the specific length of the supposed "substitution" period. Bonsall et al. (2001a) proposed that the adoption of farming in these regions is associated with the onset of drier conditions across northwest Europe, for which they adduced a range of environmental evidence, and the likely implications of drier conditions for farming productivity.

Demographic Fluctuations and Genetic Consequences

The demographic patterns that I suggest are documented in the summed radiocarbon probability curves associated with the appearance of farming in northwest Europe have more general implications for understanding the debates about the genetic legacy of the appearance of farming in Europe. Haak et al.'s

(2005) recently published study of mtDNA results from skeletons of the LBK first farmers of central Europe shows some of the issues involved. The main focus of the genetic aspect of the debate about whether farming spread to Europe as a result of demic or cultural diffusion has been on the extent to which immigrant Neolithic farmers contributed to the present-day European gene pool, unsurprisingly given that the main data have been present-day gene distributions; Haak et al.'s discussion maintains this emphasis. Their findings—that a significant proportion of the LBK skeletons are characterized by an mtDNA haplotype that is rare in present-day populations and that the decrease in frequency between 7,500 years ago and the present cannot be accounted for by any plausible drift model—are important in suggesting that female Neolithic farmers may not have contributed much to the present-day mitochondrial gene pool. However, it cannot automatically be inferred from this that demographic expansion played only a minor role in the initial spread of farming, as proponents of the cultural diffusion argument have claimed, taking it as support for previous claims to this effect on the basis of present-day gene distributions (e.g., Richards 2003). An alternative possibility suggested by the demographic proxies is that Haak et al.'s results give an indication of the potential importance of past extinction processes of a more structured nature than drift.

As we have seen, there is evidence from some areas that, however successful the LBK was to start with, it finally went demographically extinct in some regions and that the areas it had occupied were recolonized by later groups. The extent of this process is the issue that now needs to be addressed. In other words, the present-day gene distributions can tell us about expansions but little about subsequent extinctions and contractions, except to the extent that they can be encapsulated in simulations of drift models; to find out about extinctions, we need ancient DNA and archaeological evidence. Larson et al.'s (2007) recent aDNA results, which suggest that pig lineages of Near Eastern origin associated with the LBK early Neolithic went extinct while those with a local native ancestry provided the origin of more recent populations, may be relevant to human populations as well.

Conclusions

Evolutionary theory provides the basis for explaining population processes and their consequences on a variety of scales. From this perspective it is entirely predictable that people would take reproductive advantage of the opportunities for dispersal provided by the culturally (and physically) inherited cereals–pulses–domestic animals package, in a subcontinent with favorable resource patches that had low existing population densities. Similar demographic expansion processes characterize the adoption of farming in many parts of the world, as the Renfrew-Bellwood model of farming and language dispersal (see, e.g., Diamond and Bellwood 2003) makes clear, although not all agricultural systems were as productive and portable as the southwest Asian one and regional variations in agricultural-demographic trajectories are now being identified and characterized (e.g., Kohler et al. 2008). What is perhaps more novel in terms of the demographic patterns revealed in this paper is the evidence that boom was often followed by bust. It remains to be seen whether this too is a widespread phenomenon on a worldwide scale and whether we can identify the reasons for it where it occurs. In the European case examined here we do not yet know whether it was a result of extrinsic factors (such as climate change) or intrinsic factors resulting from overshooting long-term carrying capacities, with direct consequences for subsistence, and/or more indirect social factors (such as intergroup violence).

Whatever the case may be, the evidence for a decline in farming populations on the western edge of central Europe early in the 5th millennium BC calls into question the current availability-substitution-adoption model of forager-farmer interaction as a basis for explaining the spread of agriculture to northwest Europe nearly a thousand years later. Given its widespread nature, a climatically based model for the subsequent expansion of farming and farmers in northwest Europe seems more likely, although much more work needs to be done to develop and test this idea. If there was some sort of crisis of the forager system, it seems to have been restricted to southern Scandinavia (out of the regions considered here) and to have been short-lived before the switch from foraging to farming took place.

But population processes are not phenomena that are relevant only at the macroscale. On the contrary, they have profound implications on a local level and over what are, for archaeologists, short time scales. As I have tried to show in this paper, human behavioral ecology provides a spectrum of models that make theoretically based predictions of the way population processes interact with social and economic processes. Thus the ideal despotic distribution, for example, a specific implication of population ecology in the presence of territoriality, provides a basis not only for understanding settlement and colonization decisions but also, in combination with reproductive skew theory, for explaining their subsequent consequences in terms of the gradual emergence of social inequalities based on settlement priority and control of the best territories as population increased, ultimately leading, in situations that seem to approximate the late LBK, to the potential for intergroup conflict, as the growth of any given group comes to impinge on that of its neighbors, and the loss of household autonomy. The potential for using such models to explain the patterns we observe in the prehistoric past is enormous.

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Literature Cited

Ammerman, A. J., and L. L. Cavalli-Sforza. 1973. A population model for the diffusion of early farming in Europe. In *The Explanation of Culture Change*, C. Renfrew, ed. London: Duckworth, 343–357.

Berger, J.-F., and J. Guilaine. 2009. The 8200 cal BP abrupt environmental change and the Neolithic transition: A Mediterranean perspective. *Quatern. Intl.* 200(1–2):31–49.

Biagi, P., S. J. Shennan, and M. Spataro. 2005. Rapid rivers and slow seas? New data for the radiocarbon chronology of the Balkan peninsula. In *Prehistoric Archaeology and Anthropological Theory and Education*, L. Nikolova and J. Higgins, eds. Reports of Prehistoric Research Projects 6–7. Salt Lake City, UT: International Institute of Anthropology, 43–51.

Bliege Bird, R., and E. A. Smith. 2005. Signaling theory, strategic interaction, and symbolic capital. *Curr. Anthropol.* 46:221–248.

Bocquet-Appel, J. P. 2002. Paleoanthropological traces of a Neolithic demographic transition. *Curr. Anthropol.* 43:637–647.

Bocquet-Appel, J. P. 2008. Explaining the Neolithic demographic transition. In *The Neolithic Demographic Transition and Its Consequences*, J. P. Bocquet-Appel and O. Bar-Yosef, eds. New York: Springer, 35–56.

Bocquet-Appel, J. P. and S. Naji. 2006. Testing the hypothesis of a worldwide Neolithic demographic transition: Corroboration from American cemeteries. *Curr. Anthropol.* 47:341–365.

Bocquet-Appel, J. P., S. Naji, M. Vander Linden et al. 2009. Detection of diffusion and contact zones of early farming in Europe from the space-time distribution of ^{14}C dates. *J. Archaeol. Sci.* 36:807–820.

Bogaard, A. 2004. *Neolithic Farming in Central Europe*. London: Routledge.

Bogucki, P. 2003. Neolithic dispersals in riverine interior central Europe. In *The Widening Harvest: The Neolithic Transition in Europe—Looking Back, Looking Forward*, A. Ammerman and P. Biagi, eds. Boston: Archaeological Institute of America, 249–272.

Bonsall, C., M. G. Macklin, D. E. Anderson et al. 2001a. Climate change and the adoption of agriculture in northwest Europe. *Eur. J. Archaeol.* 5:7–21.

Bonsall, C., M. G. Macklin, R. W. Payton et al. 2001b. Climate, floods, and river gods: Environmental change and the Meso-Neolithic transition in southeast Europe. *Before Farming* 3–4:1–15.

Boone, J. L. 2002. Subsistence strategies and early human population history: An evolutionary ecological perspective. *World Archaeol.* 34:6–25.

Cappers, R., and D. Raemaekers. 2008. Cereal cultivation at Swifterbant? Neolithic wetland farming on the North European plain. *Curr. Anthropol.* 49:385–402.

Charnov, E. L. 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford, U.K.: Oxford University Press.

Coudart, A. 1998. *Architecture et Société Neolithique*. Paris: Editions de la Maison des Sciences de l'Homme.

Diamond, J., and P. Bellwood. 2003. Farmers and their languages: The first expansions. *Science* 300:597–602.

Dubouloz, J. 2008. Impacts of the Neolithic demographic transition on Linear Pottery Culture settlement. In *The Neolithic Demographic Transition and Its Consequences*, J. P. Bocquet-Appel and O. Bar-Yosef, eds. New York: Springer, 207–235.

Ebersbach, R., and C. Schade. 2004. Modeling the intensity of linear pottery land use: An example from the Mörlener Bucht in the Wetterau Basin, Hesse, Germany. In *Enter The Past: The E-Way into the Four Dimensions of Cultural Heritage*, Stadtarchäologie Wien, ed. BAR International Series 1227. Oxford, U.K.: Archaeopress, 337–348.

Fischer, A., J. Olsen, M. Richards et al. 2007. Coast-inland mobility and diet in the Danish Mesolithic and Neolithic: Evidence from stable isotope values of humans and dogs. *J. Archaeol. Sci.* 34:2125–2150.

Gamble, C., W. Davies, P. Pettitt et al. 2005. The archaeological and genetic foundations of the European population during the late glacial: Implications for "agricultural thinking." *Cambridge Archaeol. J.* 15(2):193–223.

Gibson, M. A., and R. Mace. 2006. An energy-saving development initiative increases birth rate and childhood malnutrition in rural Ethiopia. *PLoS Med.* 3(4):476–484.

Gillespie, D., A. Russell and V. Lummaa. 2008. When fecundity does not equal fitness: Evidence of a quantity-quality trade-off in pre-industrial humans. *Proc. R. Soc. Lond. B* 275:713–722.

Gregg, S. A. 1988. *Forager and Farmers: Population Interaction and Agricultural Expansion in Prehistoric Europe*. Chicago: University of Chicago Press.

Haak, W., P. Forster, B. Bramanti et al. 2005. Ancient DNA from the first European farmers in 7,500-year-old Neolithic sites. *Science* 310:1016–1018.

Hachem, L. 2000. New observations on the Bandkeramik house and social organization. *Antiquity* 74:308–312.

Hawkes, K., and R. R. Paine, eds. 2006. *The Evolution of Human Life History*. Santa Fe, NM: SAR Press.

Jeunesse, C. 1997. *Pratiques funéraires au néolithique ancien: Sépultures et nécropoles danubiennes 5500–4900 av. J.-C.* Paris: Errance.

Kaplan, H., K. Hill, J. Lancaster et al. 2000. A theory of human life history evolution: Diet, intelligence, and longevity. *Evol. Anthropol.* 9:156–184.

Keeley, L. H. 1992. The introduction of agriculture to the western north European plain. In *Transitions to Agriculture in Prehistory*, A. B. Gebauer and T. D. Price, eds. Madison, WI: Prehistory Press, 81–95.

Kerig, T. 2003. Von Gräbern und Stämmen: Zur Interpretation bandkeramischer Erdwerke. In *Spuren und Botschaften: Interpretationen materieller Kultur*, U. Veit, T. L. Kienlin, C. Kümmel et al., eds. Münster, Germany: Waxmann, 225–244.

Kneipp, J. 1998. *Bandkeramik zwischen Rhein, Weser und Main: Studien zu Stil und Chronologie der Keramik*. Bonn, Germany: Habelt.

Kohler, T. M. G., J.-P. Bocquet-Appel, and B. M. Kemp. 2008. The Neolithic demographic transition in the U.S. Southwest. *Am. Antiq.* 73:645–669.

Kramer, K., and J. L. Boone. 2002. Why do intensive agriculturalists have higher fertility? A household labor budget approach. *Curr. Anthropol.* 43:511–517.

Kramer, K. L., and G. P. McMillan. 2006. The effect of labor-saving technology on longitudinal fertility changes. *Curr. Anthropol.* 47:165–172.

Larson, G., U. Albarella, K. Dobney et al. 2007. Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. *Proc. Natl. Acad. Sci. USA* 104:15,276–15,281.

Lee, C. T., and S. Tuljapurkar. 2008. Population and prehistory I: Food-dependent population growth in constant environments. *Theor. Popul. Biol.* 73:473–482.

Lüning, J., and P. Stehli. 1994. *Die Bandkeramik im Merzbachtal auf der Aldenhovener Platte*. Bonn, Germany: Habelt.

Neiman, F. 1997. Conspicuous consumption as wasteful advertising: A Darwinian perspective on spatial patterns in classic Maya terminal monument dates. In *Rediscovering Darwin: Evolutionary Theory in Archaeological Explanation*, C. M. Barton and G. A. Clark, eds. Arlington, VA: American Anthropological Association, 267–290.

Niekus, M. 2009. Trapeze shaped flint tips as proxy data for occupation during the late Mesolithic and the early to middle Neolithic in the northern part of the Netherlands. *J. Archaeol. Sci.* 36:236–247.

Petrasch, J. 2001. "Seid fruchtbar und mehret euch und fullet die Erde und machet sie euch untertan . . ." *Archaeol. Korrespond.* 31:13–25.

Petrasch, J. 2005. Demografischer Wandel am Beginn der Bandkeramik. Paper presented at the conference "Die Neolithisierung Mitteleuropas," Mainz, Germany, June 24–26, 2005.

Puleston, C., and S. Tuljapurkar. 2008. Population and prehistory II: Space-limited human populations in constant environments. *Theor. Popul. Biol.* 74:147–160.

Quinlan, R. J. 2007. Human parental effort and environmental risk. *Proc. R. Soc. Lond. B* 274:121–125.

Read, D. W., and S. A. LeBlanc. 2003. Population growth, carrying capacity, and conflict. *Curr. Anthropol.* 44:59–85.

Richards, M. 2003. The Neolithic invasion of Europe. *Annu. Rev. Anthropol.* 32:135–162.

Sattenspiel, L. R., and H. C. Harpending. 1983. Stable populations and skeletal age. *Am. Antiquity* 48:489–498.

Schmidt, B., W. Gruhle, and O. Rück. 2004. Klimaextreme in Bandkeramischer Zeit (5300–5000 v. Chr.): Interpretation Dendrochronologischer und Archäologischer Befunde. *Archaeol. Korrespond.* 34:303–307.

Smith, E. A., and B. Winterhalder. 1992. Natural selection and decision making: Some fundamental principles. In *Evolutionary Ecology and Human Behavior*, E. A. Smith and B. Winterhalder, eds. New York: Aldine de Gruyter, 25–60.

Smith, M. A., and J. Ross. 2008. What happened at 1500–1000 cal. BP in central Australia? Timing, impact, and archaeological signatures. *Holocene* 18:379–388.

Strien, H. C., and D. Gronenborn. 2005. Klima- und Kulturwandel wahrend des mitteleuropaischen Altneolithikums. In *Klimaveranderung und Kulturwandel in neolithischen Gesellschaften Mitteleuropas, 6700–2200 v. Chr.*, D. Gronenborn, ed. Mainz, Germany: Verlag des Romisch-Germanischen Zentralmuseums, 131–150.

Summers, K. 2006. The evolutionary ecology of despotism. *Evol. Hum. Behav.* 26:106–135.

Sutherland, W. J. 1996. *From Individual Behavior to Population Ecology*. Oxford, U.K.: Oxford University Press.

van Andel, T. H., and C. N. Runnels. 1995. The earliest farmers in Europe. *Antiquity* 69:481–500.

van der Velde, P. 1990. Banderamik social inequality: A case study. *Germania* 68:19–38.

Vanmontfort, B. 2008. Forager-farmer connections in an "unoccupied" land: First contact on the western edge of LBK territory. *J. Anthropol. Archaeol.* 27:149–160.

Vehrencamp, S. 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behav.* 31:667–682.

Voland, E. 1998. Evolutionary ecology of human reproduction. *Annu. Rev. Anthropol.* 27:347–374.

Wahl, J., and H. G. König. 1987. Anthropologisch-traumatologische Untersuchung dermenschlichen Skelettreste aus dem bandkeramischen Massengrab bei Talheim, Kreis Heilbronn. *Fundberichte aus Baden-Württemberg* 12:65–193.

Weninger, B., K. Edinborough, M. Bradtmöller et al. n.d. A radiocarbon database for the Mesolithic and Early Neolithic in northwest Europe. Unpublished.

Wild, E. M., P. Stadler, A. Häusser et al. 2004. Neolithic massacres: Local skirmishes or general warfare in Europe? *Radiocarbon* 46:377–385.

Winterhalder, B., and D. J. Kennett. 2006. Behavioral ecology and the transition from hunting and gathering to agriculture. In *Behavioral Ecology and the Transition to Agriculture*, D. J. Kennett and B. Winterhalder, eds. Berkeley: University of California Press, 1–21.

Winterhalder, B., and E. A. Smith. 2000. Analyzing adaptive strategies: Human behavioral ecology at twenty-five. *Evol. Anthropol.* 9:51–72.

Wood, J. W. 1998. A theory of preindustrial population dynamics: Demography, economy, and well-being in Malthusian systems. *Curr. Anthropol.* 39:99–135.

Zimmermann, A. 2002. Landschaftsarchäologie I Die Bandkeramik auf der Aldenhovener Platte. *Bericht der Romisch-Germanischen Kommission* 2002:17–38.

Zvelebil, M., 1996. The agricultural frontier and the transition to farming in the circum-Baltic region. In *The Origins and Spread of Agriculture and Pastoralism in Eurasia*, D. R. Harris, ed. London: University College London Press, 323–345.

Zvelebil, M., and P. Rowley-Conwy. 1986. Foragers and farmers in Atlantic Europe. In *Hunters in Transition: Mesolithic Societies of Temperate Europe and Their Transition to Farming*, M. Zvelebil, ed. Cambridge, U.K.: Cambridge University Press, 67–93.