# The spread of farming into Central Europe and its consequences: evolutionary models

## Stephen Shennan

AHRC Centre for the Evolutionary analysis of Cultural Behaviour and Institute of Archaeology, UCL. 31-34 Gordon Sq. London WC1H oPY, UK. email: s.shennan@ucl.ac.uk

#### Introduction

The use of Darwinian evolutionary models to understand patterns of social, economic and cultural change in the prehistoric past is becoming increasingly well established [e.g. 35, 22, 11, 21, 23, 15, 32]. However, it remains the subject of many misconceptions [e.g. 19], both because of the erroneous assumptions that those unfamiliar with evolutionary theory bring to their reading of the evolutionary literature, and also because of the inherent complexity of the whole endeavour. The complexity is unsurprising in the light of the history of biology over the past 150 years where the substantive and philosophical implications of Darwinism continue to ramify [e.g. 16]. In the case of the application of these ideas to the study of human societies and their history we are far nearer the beginning of the process of developing appropriate theory and the subject matter is more complex (although there are increasing suggestions that the complexity of inheritance in animal populations has been underestimated [e.g. 20, 10, 16]. Moreover, different topics call on different aspects of evolutionary theory.

In this paper I will look at two different inter-related topics that have long been of interest to archaeologists of virtually all theoretical persuasions and examine how evolutionary theory can be used to illuminate them by presenting a specific concrete example. The two topics concern the history of human populations, the history of social institutions and the link between the two. Much less emphasis will be placed on two other types of histories for the understanding of which Darwinian theory is equally illuminating, histories of culturally transmitted norms, practices and artefact attributes, and the process of 'niche construction': the fact that the activities of the current generation produce outcomes, new environments, that change the selection pressures operating on subsequent ones.

Obviously, the basis for describing and explaining these histories from an evolutionary perspective is the establishment of a connection between them and relevant processes and entities in evolutionary theory. There must be an inheritance mechanism, a means of generating novelty, and processes that affect the frequency with which things are represented in future generations.

In the case of the cultural practices of interest to archaeologists the inheritance mechanism is social learning and novelty is produced by innovation. The latter can be mere copying error but it can also arise from trial-and-error experimentation that leads individuals to give up what they were originally doing and do something else, in the belief that it produces better results in some sense. This does not mean that problems always call into being their solutions: necessity may be one of the mothers of invention but it is not necessarily the mother of successful invention. Success depends on a variety of processes, one of which is natural selection.

The operation of natural selection needs some unpacking in the human case. In the first place it assumes that humans, like other animals, have evolved to have a propensity to maximise their reproductive success, and to be able to recognise and respond to variations in their environment relevant to achieving it. This leads to the assumption that at the level of the day-to-day business of getting a living the principles of optimal foraging should hold. Subject to these, if changed conditions of some kind alter the trade-offs involved in achieving reproductive success, people will respond to them, increasing their fertility in good times and decreasing it when times are hard.

But natural selection can also act on people via their cultural traditions. In other words, particular inherited cultural beliefs and practices may lead to some people having greater survival rates and reproductive success than others. If they also transmit these successful beliefs/practices to their children their prevalence will increase and will in turn again increase the reproductive success of the children that practise them, for as long as those practices are advantageous.

A further cultural twist on natural selection also exists [7, 27]. A particular set of beliefs or practices may lead an individual not to greater reproductive success and associated transmission of the successful beliefs to children, but to greater success as a model to be copied in various respects. If the practices/beliefs that made the individual a successful model to be copied are adopted by the copiers, they too will be more likely to be models for the beliefs and practices of subsequent generations. Whereas in the first case there is competition between cultural attributes that affects who will be the biological parents of the next generation, in this case the competition is about who will be its 'cultural parents'.

However, the frequencies of beliefs and practices through time are also affected by what Boyd and Richerson [7] have called decision-making biases. These include the preferential copying of practices because they appear to give better results in some sense (directly-biased transmission)

and the preferential copying of practices simply because they are common (conformist transmission). There may be complex feedbacks between all these different processes. A conformist bias, for example, may lead not simply to greater replicative success for one particular belief/practice as opposed to another, it might have deleterious effects on the reproductive success of members of a community if it means that they respond more slowly than would be beneficial to changes, for example, in the natural environment. On the other hand, if in general those who conform tend to be more successful in obtaining a partner and bringing up children, then a process of gene-culture co-evolution may develop if relevant aspects of human psychology are genetically influenced.

A special position in analyses of natural selection and culture is occupied by evolutionary game theory [e.g. 33] focussed on the competition between strategies of social interaction in terms of the pay-offs they give to the interactors in different social situations. Here what is changing through time as a result of differential pay-offs is the frequency of social strategies in a population, but obviously this too may have survival/reproductive success consequences for the practitioners of the strategies, and also for the replicative success of the norms associated with the favouring of particular strategies.

Last but not least in terms of the evolutionary processes that affect the frequency of transmitted cultural practices over time is drift: the effect of chance variation in the frequency with which practices are copied, unrelated to their properties. The idea that drift is relevant to understanding cultural change has a long history in anthropology and archaeology [e.g. 28, 3], but its significance was most explicitly argued by Dunnell [12] in his distinction between style and function in artefacts, the latter referring to all variation that is under selection and the former to that which is not, i.e. is neutral. For Dunnell this was an absolute distinction – attributes were either under selection or they were not – but, in fact, even if particular attributes are under selection, their representation in subsequent generations may be almost entirely the result of chance factors if population sizes are small.

It will by now be apparent why the evolutionary understanding of histories of norms, populations and social institutions is so complex. The histories are inter-connected, but certainly not reducible to one another, while processes affecting one can also have repercussions for the others, not to mention potential effects on the genetic constitution of populations. For prehistory the situation is further complicated by the fact that some of these histories are relatively inaccessible. Archaeologists have been tracing the histories of norms of artefact production with considerable success since the discipline began, but as yet we have very little direct information about the history of populations because at the moment we lack the means to establish who was

the biological descendant of whom, except in very exceptional cases. Inferences on this subject depend on assumed links between people and their traditions which have been known for decades to be problematical, for reasons arising from the wide range of routes of cultural transmission. Tracing the history of social institutions is also difficult, although it is one of the main areas in which anthropological archaeologists have made progress in the last 40 years.

The alternative to reacting to these complexities with despair is to use evolutionary models based on well-founded assumptions to address specific archaeological issues. The example that will be investigated here, following this approach, is the rise and decline of the first farming societies in Central Europe, c.5600-4900 BC, in the context of the broader phenomenon of the spread of cereal-based agriculture from its Near Eastern origins to northwest Europe. The starting point is a demographic one.

## **Demographic processes**

If the history of human population in a given region were simply a very gradual rise over the long-term, then arguably population processes could be left out of account in our attempts to understand patterns of change and continuity in human history. In fact, it is increasingly clear that local populations have fluctuated very considerably in response to a variety of endogenous and exogenous factors [cf. 31]. As human populations are the fundamental support for all cultural processes, it is essential both to document those fluctuations and to explain them.

The mechanism behind population processes is natural selection. Humans, like other animals, have evolved to maximise their reproductive success. The idea that children are a good in themselves, rather than simply a means to an end, for example to increase the pool of agricultural labour (although this may well be relevant to the specific costs and benefits of bringing up children), seems to be held in virtually all human cultures. Some people have been more successful than others at surviving, finding a mate and bringing up their children and have left more descendants as a result [see e.g. 30, 46 for striking examples].

In these circumstances, given that there are always trade-offs between the maximum number of children that you can produce and the maximum that you can bring to the stage of being successful parents themselves, 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. 45]. Those changed conditions may be entirely exogenous, for example climatic variations, or

stem from innovations leading to new adaptations. Thus, a regional population increase, unless it is a point on a curve of endogenous cyclical fluctuations, is likely to be an indicator of new conditions promoting increased reproductive success. Population stability is an indication that a local ceiling has been reached, a process that will not take very long given the rapid increases in numbers that even relatively low growth rates produce.

New adaptations will be especially successful if dispersal opportunities are available to the human populations practising them [43], so that when a local population ceiling has been reached expansion can continue elsewhere. The spread of farming into Europe can be regarded as 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 very low. However, the areas with low population densities included zones that were very suitable for growing cereal crops and could thus sustain much higher densities of farmers than huntergatherers. 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 subsumed the small hunter-gatherer populations existing in the areas initially occupied by early farmers. In other words, this is a classic example of natural selection acting on people through an inherited cultural tradition, which gave a selective advantage to those who adopted it and passed it on to their children; in fact, in this case it was not simply a tradition that was inherited but the actual descendants of the cereal crops and animals that had originally been domesticated.

The visible evidence of this process is seen not only in the greatly increased density of human settlement in those areas where farming arrived, but also in the demographic profiles of cemeteries, as Bocquet-Appel [5] has shown (see fig. 1). The zero point on the horizontal axis of fig 1 marks the time of arrival of cereal agriculture at a given place. To the left, time before the arrival of farming at that place increases, to the right, time after its initial arrival. The figure shows that prior to the arrival of farming population growth rates inferred from cemetery populations were at or just below replacement level; afterwards they were growing, albeit at varying rates.

On the basis of studies of the number, size and density of settlements of the Linear Pottery Culture in Central Europe Petrasch [25, 26] has calculated population growth rates between 0.9% and 2.7% for the first farming societies in this area.

In detail, the expansion process seems to have involved the colonisation of patches favourable to the new economy, rather than uniform expansion [40], hence the rapidity with which it occurred in many areas [see 47 for the north Mediterranean coast].

### The ideal despotic distribution

There has been a tendency to assume 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 Europe and documented by the fact that in certain areas we can see that new places were colonised before others reached any sort of carrying capacity (see below). The basis for understanding why further expansion does not necessarily presuppose demographic saturation is again provided by principles derived from thinking through the implications of natural selection, in this case as they relate to decision-making concerning spatial behaviour. Here the principle in question is the 'ideal despotic distribution' from population ecology [37]. The 'ideal free distribution' proposes that individuals occupy the resource patch which gives them the best returns. 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 has no occupants. Now the returns from both patches are equal and they will be occupied indiscriminately until such time as the population grows to the point at which there is an equal benefit to be gained by occupying a still worse patch, and the process is repeated.

<sup>&</sup>lt;sup>1</sup> In the context of the extensive recent debates about the proportion of 'Palaeolithic' or 'Neolithic' genes in present-day European populations it is worth noting that recent simulations of the expansion of farming into Europe show that even very low rates of genetic interaction between hunter-gatherers and farmers, under the assumption of much higher population densities for farmers than hunter-gatherers, still produce a situation in which present-day European populations are largely characterised by genes of local Palaeolithic ancestry (Currat and Excoffier 2005).

When there is territoriality, however, the situation is different. Here the 'ideal despotic distribution' applies (fig. 2). The first individual occupying the 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 where 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 the case of the 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, that is, as they can defend the territory against anyone who might seek to take it from them.

It is proposed then that in the case of 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.

#### The first farmers in Central Europe

By the beginning of the 6<sup>th</sup> millennium cal.BC groups with agricultural economies had spread through southeast Europe into the Carpathian Basin. The so-called Linear Pottery Culture (or LBK after its German name) which characterises the first farming groups of Central Europe appears to have originated in western Hungary/ eastern Austria c.5600-5500 cal.BC. It spread extremely quickly westwards. The area covered by the earliest LBK (see fig 3), although it appears that it should now be extended still further west [14] seems to have been settled in less than 150 years [25], although it should be emphasised that the occupation was not spatially continuous but restricted to particular patches. Across this broad area the earliest pottery is extremely uniform [8]. Subsequently the area expanded still further, as fig. 3 shows. The LBK seems to have ended c.5000-4900 cal.BC, later in some areas than others [36].

Detailed fieldwork in Germany in the western Rhineland enables this process to traced at a local scale (summarised in [49]). Fig 4 shows part of the sequence of occupation on the Aldenhovener Platte. Occupation began at the site of LW8 in phase 1 of the local LBK sequence (fig 4a). LW8 subsequently expanded and new settlements were founded adjacent to it but the local carrying capacity was not reached until later (fig 5; and see below). In the meantime,

however, already in phase 2, as fig 4b indicates, other favourable local micro-areas were being settled. The founding settlements in particular areas remained the dominant ones. LW8, for example, was occupied throughout the c.400 years of the local LBK sequence and was always the largest. Apart from its presumptively best location from the farming point of view, it also seems to have been a redistribution centre 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 [49, 17]. Moreover, it was at LW8 that a ditched enclosure of possible ritual significance was constructed in the latest local phases of LBK occupation.

Over time these local LBK societies 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 [41], on the basis of sites in the southeastern Netherlands and the Aldenhovener Platte discussed above. LBK houses seem to be made up of three modules with different functions: a northwest, central and southeastern part. Some houses only have 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 proposes that the distinctions between houses with larger and smaller numbers of elements relate to the wealth and status of their associated households and cannot be explained by changing household composition arising from family life-cycles or qualitatively different household compositions [41]. 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 site of LW8 cereal processing waste was preferentially associated with the large houses [6]. Elsewhere there is evidence of higher proportions of domestic animal bones being associated with large houses and more remains of hunted animals with smaller ones [13]. On the basis of a spatial analysis of the settlements he studied, van der Velde also shows that the units of which the settlements were made up 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 [9] analysis of LBK houses leads her to conclude that major rank or wealth differentiation did not exist but she too points to some indications of status differences. She notes, for example, [9] that granaries were never associated with small houses and that some buildings were more spacious than others. Interestingly, she also suggests 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 also the existence of separate cemeteries, mainly of individual inhumations, which are very rare in the earliest LBK phases. Jeunesse [17] concludes that the earliest ones present a picture of relatively egalitarian societies, with indications of achieved status for older men, while the later ones 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 that belonged to the settlements of the Merzbachtal on the Aldenhovener Platte.

The evidence for social differentiation, or the lack of it, has generally been discussed in terms of concepts from neo-evolutionary theory, for example the existence of 'big men' [9, 41], but in my view the key to understanding the patterns that may be discerned in the settlements and cemeteries lies in the ideal despotic distribution discussed above, where it was invoked to account for the rapid spread of the LBK farming system and its bearers in a context of rapid population growth, in a situation where people had the option of moving on to new unoccupied patches rather than having to accept inferior territories in areas that had already been occupied.

The first comers to favourable settlement micro-regions were able to settle in the best locations. Despite the high population growth rate there was no competition between different groups because, as new households were formed, they were able to move to favourable locations elsewhere – indeed, this is what made the population growth possible. Relatively rapidly though, as the Merzbach evidence shows (fig 5), the individual micro-regions began to fill up. This did not affect the suitability of the area for those who had already established themselves there, because success depended on having a territory and they controlled the best ones. 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 [42] and Kneipp [18] (cited by [49]) to account for the establishment of the Niedermerz 3 cemetery on the Aldenhovener Platte in the 52<sup>nd</sup> century cal.BC.

What the limits on carrying capacity were is unclear. Zimmermann [49] has argued that there would have been more than enough land available for the small-scale intensive garden agriculture that was most probably practised, and which in itself is likely to imply some form of land ownership [6], but that ensuring the availability of fodder for cattle would have required very large territories. As fig 5 shows, the evidence that it *was* reached is the clear ceiling in the number of Merzbach houses, supported by the recent suggestion, also shown in fig 5, that the fluctuations

in house totals, once an initial ceiling had been reached, were affected by local climatic patterns [29]; if confirmed, this would also point to the fragility of LBK subsistence at the limit.

Strontium isotope analyses [2] suggest that in the early phases of the LBK there was fairly general mobility but that in the later phases it was mainly women that moved. This would point to the emergence of patrilineal corporate groups. One can therefore postulate that over time the senior line of the lineage in a given micro-area would have maintained control of the prime location and its territory and is represented archaeologically by the larger houses in the settlements. The junior branches, on the other hand, would be in increasingly inferior positions and would have relatively little option to go elsewhere because the same process was going on everywhere around them, hence the increasing number of smaller houses that van der Velde noted.

One can further speculate that once local micro-regions became full, contest competition between lineages would have become increasingly important and members of the senior line would increasingly have had to assert their position in order to maintain it. The deposition of rich grave goods as a form of costly signalling [23, 4] would probably have had a role here. In this case, the number of rich burials would not simply be a reflection of the size of the senior lineage but of the competitive pressure it was under in particular places and times.

It is not clear whether the processes described above occurred throughout the LBK distribution but they certainly seem to have been prevalent in its western half on the basis of the evidence and sources cited above. 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 the LBK settled. Second, all these local societies ultimately had a common origin and thus a very similar starting point in terms of social norms and institutions. This is very apparent in the material dimensions for which we have evidence. As noted already, the pottery of the earliest LBK is extremely uniform across a very large area, and the uniformity of the houses is equally striking. However, it is also clear that there was continuing contact between LBK communities, subsequent to the initial colonisation. This is evident not merely in lithic and other exchange networks [48] but also in the fact that innovations, for example in pottery decoration, are not entirely localised but spread across large areas [e.g. 36].

#### The decline of the LBK

The emergence of local inequality in terms of hereditary social and economic distinctions based on priority of access to the best territories during the colonisation process, is not the only widespread institutional trend to be observed in the course of the LBK. The appearance of an apparently ceremonial enclosure in the late phases of the founding settlement. LW8, in the Merzbachtal has already been mentioned, and it is not an isolated occurrence. The pattern of later occupation phases with ditched and/or palisaded enclosures seems to characterise many settlements of the LBK farmers. There has been considerable discussion of the function of these late enclosures. The idea that defence was often among them has been supported in recent years by the finding of two massacre sites dated to local late LBK phases [44, 38]. But this was not their only role. Some certainly have ritual significance, for example evidence of special burial rituals [24].

Kerig (2003) has suggested that the enclosures represent the emergence of a new type of social institution integrating larger numbers of people into a single social unit, which would presumably have been integrated with the patrilineal land-holding lineage system that has been postulated above. 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 massacres [44, 38]. In the former case the remains of 34 individuals were recovered, in the latter case at least 67, even though not all the enclosure ditch was fully excavated. These figures imply very large numbers of attackers.

One possible analogy comes from Barth's description of the Faiwolmin group in New Guinea [1, quoted in 34; see also Tuzin's [39] description of an analogous situation with the New Guinea Abelam and Arapesh). Barth pointed out that the western Faiwolmin communities lived in nucleated villages centred on cult houses, while in the east populations were dispersed. The centralised communities thus had a military advantage and as a result were able to expand towards the east, where the social system could not organise as many people for defence.

Thus, 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. In the 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 there was competitively successful, other groups had little opportunity but to copy them if they wished to avoid potentially disastrous consequences. The general context in which to see this is the reaching of local carrying capacities in many of the areas where LBK farmers had settled, and the apparent vulnerability of the farming system in these circumstances to climatic stresses such as those suggested by [29].

The emergence of enclosures is not the only indicator of change in the late LBK. Long-distance lithic exchange also declined. Through most of the LBK period supplies of high-quality flint were obtained from special sources and exchanged very widely. In the latest phase exchanged lithic raw material declined in frequency at settlement sites and increasing proportions of the lithic assemblages were made of material from local sources of poorer quality. It may be that relations between adjacent groups broke down so completely that long-distance exchanges, with material going through many hands, simply became impossible.

Whatever the reasons for it, it is clear that c.5000-4900 there was a widespread collapse of the LBK system, although this was not simultaneous in all areas. In at least some regions where the detailed work has been done, such as the Aldenhovener Platte, it is apparent that there was a general demographic collapse and it was largely if not entirely abandoned for c.100 years; when it was reoccupied the settlement pattern was a much more nucleated one. New Middle Neolithic systems seem to have originated in limited areas of the existing LBK and their spread seems to have involved, at least in part, re-colonisation processes, new demographic expansions, albeit on a much smaller scale than that which produced the LBK in the first place.

## **Conclusions**

While complex evolutionary processes are at work in human populations, many of them with no parallel or little importance in non-human species, a great deal can be understood about the mechanisms involved in the spread of farming into Europe and their consequences by starting from some very basic assumptions arising from the theory of natural selection. First, 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 sub-continent with favourable resource patches which had very low existing population densities; they would have absorbed existing populations as they went. In more detail, the ideal despotic distribution, a specific ecological implication of natural selection, provides a basis not only for understanding settlement and colonisation decisions but also 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. In turn, costlysignalling theory in a situation of contest competition for the best territories offers a framework for understanding the growing differentiation in grave goods and its apparently hereditary dimension, indicated by child graves with rich grave goods. Previous workers, such as van der Velde [41], have made suggestions in a similar direction, from a neo-evolutionary perspective, but without placing them in the integrated theoretical framework offered by Darwinian theory. However, it seems unlikely that there would have been such widespread parallel development in the LBK had it not been for the fact that the norms and institutions of local communities had a recent common origin: the patterns identified here do not appear to be universal in the European early Neolithic.

With regard to the demise of the LBK and the beginning of the Middle Neolithic, it is still unclear how far, and in what regions, it involved only the collapse of a cultural pattern and a set of institutions, and the emergence or spread of new ones, and how far it involved local population collapses and re-colonisations. In understanding these contrasting trajectories the roles of entirely exogenous factors, such as drought, and of such internal processes as warfare remain to be disentangled and their possible interactions explored from an evolutionary perspective.

#### Acknowledgements

I would like to thank Tim Kohler for the opportunity to attend the SFI Workshop on Modelling Long-Term Culture Change, from which I learned a great deal; my colleagues and students at the AHRC Centre for the Evolutionary Analysis of Cultural Behaviour for their continuing stimulus; Andreas Zimmmermann for the copy of his important 2002 paper; and Detlef Gronenborn and Joerg Petrasch for the opportunity to attend the conference *Die Neolithisierung Mitteleuropas*.

#### References

- 1. Barth, F. "Tribes and intertribal relations in the Fly headwaters." *Oceania* 41 (1971): 171-191.
- 2. Bentley, R.A., T.D. Price, J. Lüning, D. Gronenborn, J. Wahl and P.D. Fullagar. "Human Migration in Early Neolithic Europe." *Current Anthropology* **43** (2002): 799-804.
- 3. Binford, L. "'Red Ochre' Caches from the Michigan Area: A Possible Case. of Cultural Drift." *Southwestern Journal of Anthropology* **19** (1963): 89–108.
- 4. Bliege Bird, R. and E.A. Smith. "Signaling Theory, Strategic Interaction, and Symbolic Capital." *Current Anthropology* **46** (2005): 221-248.

- 5. Bocquet-Appel, J.P. "Paleoanthropological Traces of a Neolithic Demographic Transition. *Current Anthropology* **43** (2002): 637-647.
  - 6. Bogaard, A. Neolithic Farming in Central Europe. London: Routledge, 2004.
- 7. Boyd, R. and P.J. Richerson. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press, 1985.
- 8. Cladders, M. Die Tonware der Ältesten Bandkeramik: Untersuchung zur Zeitlichen und Räumlichen Gliederung. Bonn: Habelt, 2001.
- 9. Coudart, A. 1998. *Architecture et Société Néolithique*. Paris: Éditions de la Maison des Sciences de l'Homme, 1998.
- 10. Danchin, E., L.A. Giraldeau, T. J. Valone, R.H. Wagner. "Public Information. From Nosy Neighbors to Cultural Evolution." *Science* **305** (2004): 487-491.
- 11. Dominguez, S. "Optimal Gardening Strategies: Maximizing the Input and Retention of Water in Prehistoric Gridded Fields in North Central New Mexico." *World Archaeology* **34** (2002): 131-163.
- 12. Dunnell, R. "Style and Function: a Fundamental Dichotomy." *American Antiquity* **43** (1978): 192-202.
- 13. Hachem, L. "New observations on the Bandkeramik house and social organisation." *Antiquity* **74** (2000): 308-12.
- 14. Heinen, M. "Niederkassel-Uckendorf: Neue Erkenntnisse zum Beginn des Neolithikums im Rheinland." Paper presented at the conference *Die Neolithisierung Mitteleuropas*, Mainz, Germany, 24-26 June 2005.
- 15. Holden, C., and R. Mace. "Spread of Cattle Led to the Loss of Matriliny in Africa. A Coevolutionary Analysis." *Proceedings of the Royal Society B* **270** (2003): 2425-2433.
- 16. Jablonka, E., and M.J. Lamb. Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life. Cambridge, Mass.: Bradford Books, 2005.

- 17. Jeunesse, C. Pratiques Funéraires au Néolithique Ancien: Sépultures etNécropoles Danubiennes 5500-4900 av. J.-C. Paris: Errance, 1997.
- 18. Kneipp, J. Bandkeramik zwischen Rhein, Weser und Main. Studien zu Stil und Chronologie der Keramik. Bonn: Habelt, 1998.
- 19. Kristiansen, K. "Genes versus Agents. A Discussion of the Widening Theoretical Gap in Archaeology." *Archaeological Dialogues* **11** (2004): 77-99.
- 20. Laland, K.N., J. Odling-Smee and M.W. Feldman. "Niche Construction, Biological Evolution, and Cultural Change." *Behavioral and Brain Sciences* 23 (2000): 131-145.
- 21. Lyman, R. L. and M. J. O'Brien. "Measuring and Explaining Change in Artifact Variation with Clade-Diversity Diagrams." *Journal of Anthropological Archaeology* **19** (2000): 39-74.
- 22. Nagaoka, L. "Explaining Subsistence Change in Southern New Zealand Using Foraging Theory Models." *World Archaeology* **34** (2002), 84-102.
- 23. Neiman, F. "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*, edited by C.M. Barton and G.A. Clark, 267-290. Arlington, Virginia: American Anthropological Association, 1997.
- 24. Orschiedt, J., A. Häußer, M.N. Haidle, K.W. Alt, C.H. Buitrago-Téllez. "Survival of a multiple skull trauma: the case of an early neolithic individual from the LBK enclosure at Herxheim (Southwest Germany)." *International Journal of Osteoarchaeology* **13** (2003): 375-383.
- 25. Petrasch, J. "Seid fruchtbar und mehret euch und fullet die Erde und machet sie euch untertan'. …" Archaeologisches Korrespondenzblatt 31 (2001): 13–25.
- 26. Petrasch, J. "Demografischer Wandel am Beginn der Bandkeramik." Paper presented at the conference *Die Neolithisierung Mitteleuropas*, Mainz, Germany, 24-26 June 2005.

- 27. Richerson, P.J. and R. Boyd. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press, 2004.
  - 28. Rivers, W.H.R. Psychology and ethnology. London: Kegan Paul, Trench, Trubner, 1926.
- 29. Schmidt, B., W. Gruhle and O. Rück "Klimaextreme in Bandkeramischer Zeit (5300-5000 v. Chr.): Interpretation Dendrochronologischer und Archäologischer Befunde." Archäologisches Korrespondenzblatt 34 (2004): 303-307.
- 30. Scriver, C.R. "Human Genetics: Lessons from Quebec Populations." *Annual Review of Genomics and Human Genetics* 2 (2001): 69-101.
- 31. Shennan, S.J. "Population, Culture History and the Dynamics of Culture Change." *Current Anthropology* **41** (2000), 811-835.
- 32. Shennan, S.J. *Genes, Memes and Human History: Darwinian Archaeology and Cultural Evolution*. London: Thames and Hudson, 2002.
- 33. Skyrms, B. 1996. Evolution of the Social Contract. Cambridge: Cambridge University Press.
- 34. Soltis, J., R. Boyd and P. Richerson 1995. "Can Group-Functional Behaviours Evolve by Cultural Group Selection? An Empirical Test. *Current Anthropology* **36** (1995): 473-493.
- 35. Stiner, M.C. and N.D. Munro. "Approaches to Prehistoric Diet Breadth, Demography, and Prey Ranking Systems in Time and Space." *Journal of Archaeological Method and Theory* 9 (2002): 181-214.
  - 36. Strien, C. Untersuchungen zur Bandkeramik in Württemberg. Bonn: Habelt, 2000.
- 37. Sutherland, W.J. From Individual Behaviour to Population Ecology. Oxford: Oxford University Press, 1996.
- 38. Teschler-Nicola, M., F. Gerold, M. Bujatti-Narbeshuber, T. Prohaska, Ch.Latkoczy, G. Stingeder and M. Watkins. "Evidence of Genocide 7000 BP Neolithic Paradigm and Geoclimatic Reality." *Coll. Antropol.* **23** (1999): 437-450.

- 39. Tuzin, D. Social Complexity in the Making: A Case Study among the Arapesh of New Guinea. London: Routledge, 2001.
- 40. van Andel, T.H., and C.N. Runnels. "The Earliest Farmers in Europe." *Antiquity* **69** (1995): 481-500.
- 41. van der Velde, P. "Banderamik Social Inequality a Case Study." *Germania* **68** (1990): 19-38.
- 42. van der Velde, P. "Dust and Ashes: the Two Neolithic Cemeteries of Elsloo and Niedermerz Compared." *Analecta Praehistorica Leidensia* **25** (1996): 173-188.
- 43. Voland, E. "Evolutionary Ecology of Human Reproduction. *Annual Review of Anthropology* **27** (1998): 347-374.
- 44. Wahl, J., and H.G. König 1987. "Anthropologisch-traumatologische Untersuchung der menschlichen Skelettreste aus dem bandkeramischen Massengrab bei Talheim, Kreis Heilbronn." Fundberichte aus Baden-Württemberg 12 (1987): 65-193.
- 45. Wood, J.W. 1998. "A Theory of Preindustrial Population Dynamics Demography, Economy, and Well-being in Malthusian Systems. *Current Anthropology* **39** (1998): 99-135.
- 46. Zerjal, T., Y. Xue, G. Bertorelle, R. Spencer Wells, W. Bao, S. Zhu, R. Qamar, Q. Ayub, A. Mohyuddin, S. Fu, P. Li, N. Yuldasheva, R. Ruzibakiev, J. Xu, Q. Shu, R. Du, H. Yang, M.E. Hurles, E. Robinson, T. Gerelsaikhan, B. Dashnyam, S. Mehdi and C. Tyler-Smith. "The Genetic Legacy of the Mongols." *American Journal of Human Genetics* **72** (2003): 717-721.
- 47. Zilhao, J. "Radiocarbon Evidence for Maritime Pioneer Colonization at the Origins of Farming in West Mediterranean Europe." *Proceedings of the National Academy of Sciences U S*48. (2001):14180-5.
- 48. Zimmermann, A. *Austauschsysteme von Silexartefakten in der Bandkeramik Mitteleuropas*. Bonn, Habelt, 1995.
- 49. Zimmermann, A. 2002. "Landschaftsarchäologie I Die Bandkeramik auf der Aldenhovener Platte." *Bericht der Römisch-Germanischen Kommission* (2002): 17-38.

#### Figure captions

Fig 1 Estimated proportions of individuals in the age 5-19 category from a series of Mesolithic and Neolithic cemeteries in Europe, with a best fit line produced by Loess fitting. The dashed line shows a value corresponding to a population growth rate of zero. The zero point on the horizontal axis marks the estimated time of arrival of cereal agriculture at a given place. To the left, time before the arrival of farming at that place increases, to the right, time after its initial arrival. From Bocquet-Appel 2002.

Fig 2 The ideal despotic distribution. Due to territoriality the suitability of a patch for each individual decreases with the order of settling. Subsequent individuals do not affect the quality of the territories of those who settled first. Individuals settle in the better patch until point A, at which a new arrival does equally well by taking the best position in the worse patch. Later individuals settle equally in both patches. However, the average return differs between the patches. From Sutherland 1996.

Fig 3. The distribution of the LBK. The dark shading represents the distribution of the earliest LBK, the light shading the later LBK. From Zimmermann 2002.

Fig 4 a) Simplified soil map of the eastern Aldenhovener Platte showing the first LBK house generation. At LW8 there are already 4 houses; the other major settlements perhaps begin a house generation earlier or later and are indicated by a question mark. The empty squares mark the location of later subsidiary settlements.

b) As 4a but showing the situation at house generation II.

From Zimmermann 2002.

Fig 5 Reconstruction of variation in precipation in western Europe between 5600 and 4600 cal.BC on the basis of an homogeneity analysis of oak tree-ring data. After a very dry phase at c. 5360 BC (marked 1 on the figure) the following phases are wetter. After the third wet phase there is another dry period (marked 2), which corresponds with the end of the LBK. There is another dry phase c.4700 BC. The histogram in the figure shows the chronological distribution of the LBK houses from the Merzbach valley. The correspondence between the variations in precipitation and in the number of houses is striking. From Schmidt et al. 2004.