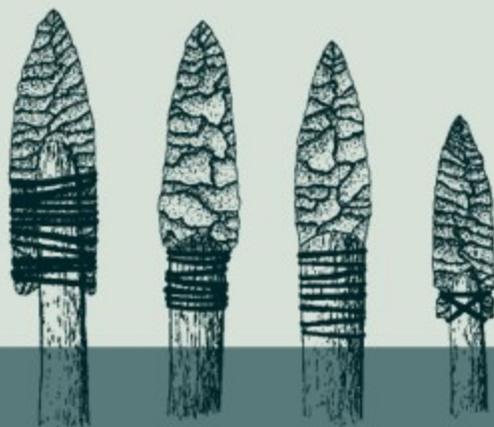


The Vienna Series in Theoretical Biology



Innovation in Cultural Systems

Contributions from Evolutionary Anthropology

edited by
Michael J. O'Brien and
Stephen J. Shennan



Innovation in Cultural Systems

Vienna Series in Theoretical Biology

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Series Foreword

Biology is becoming the leading science in this century. As in all other sciences, progress in biology depends on interactions between empirical research, theory building, and modeling. However, whereas the techniques and methods of descriptive and experimental biology have evolved dramatically in recent years, generating a flood of highly detailed empirical data, the integration of these results into useful theoretical frameworks has lagged behind. Driven largely by pragmatic and technical considerations, research in biology continues to be less guided by theory than seems indicated. By promoting the formulation and discussion of new theoretical concepts in the biosciences, this series is intended to help fill the gaps in our understanding of some of the major open questions of biology, such as the origin and organization of organismal form, the relationship between development and evolution, and the biological bases of cognition and mind.

Theoretical biology has important roots in the experimental biology movement of early-twentieth-century Vienna. Paul Weiss and Ludwig von Bertalanffy were among the first to use the term *theoretical biology* in a modern scientific context. In their understanding the subject was not limited to mathematical formalization, as is often the case today, but extended to the conceptual problems and foundations of biology. It is this commitment to a comprehensive, cross-disciplinary integration of theoretical concepts that the present series intends to emphasize. Today, theoretical biology has genetic, developmental, and evolutionary components, the central connective themes in modern biology, but also includes relevant aspects of computational biology, semiotics, and cognition research and extends to the naturalistic philosophy of sciences.

The “Vienna Series” grew out of theory-oriented workshops, organized by the Konrad Lorenz Institute for Evolution and Cognition Research (KLI), an international center for advanced study closely associated with the University of Vienna. The KLI fosters research projects, workshops, archives, book projects, and the journal *Biological Theory*, all devoted

to aspects of theoretical biology, with an emphasis on integrating the developmental, evolutionary, and cognitive sciences. The series editors welcome suggestions for book projects in these fields.

Gerd B. Müller, University of Vienna and KLI

Günter P. Wagner, Yale University and KLI

Werner Callebaut, Hasselt University and KLI

Preface and Acknowledgments

Innovation has long played a significant role in the social sciences in structuring arguments about how and why human behavior changes. Certainly innovation was implicit in the nineteenth-century writings of ethnologists such as Edward B. Tylor and Lewis Henry Morgan, as it was in the mid-twentieth-century work of Julian Steward and Leslie White. For these cultural evolutionists, the appearance of cultural innovations was almost a pre-programmed process, which kicked in whenever a cultural group “needed” to overcome social- or physical-environmental problems. Archaeological explanations of cultural change, too, have long centered around the introduction and spread of novelties. American culture historians of the twentieth century routinely looked to diffusion and trade as a source of innovations, in the process adopting, often without comment, the models of their ethnological colleagues as to how and why the innovations arose in the first place.

With the renewed interest in evolution that became noticeable in the social sciences, particularly ethnology and archaeology, in the 1980s, researchers began to reconsider the role of innovation in the evolution of cultural systems. Importantly, modern evolutionary research in the social and behavioral sciences is being geared toward identifying innovation not only as a product but also as a process. In that vein, a recent workshop at the Santa Fe Institute, New Mexico, centered on the issue of innovation, building on the work of Austrian economist Joseph Schumpeter, who made the distinction between invention—the creation and establishment of something new—and innovation—an invention that becomes economically successful and earns a profit. This distinction had been made previously in biology—introduction of a novelty versus long-term success of a species—but not in the social sciences. There, the long-held belief that humans were somehow exempt from Darwinian processes such as natural selection ensured that the only brand of evolutionism discussed was of the unilinear Tylor–Morgan–White brand.

To build on the growing body of work on cultural innovation, we organized a workshop at the Konrad Lorenz Institute for Evolution and Cognition Research (KLI) in Altenberg, Austria, in September 2007. We adopted something of a similar topical approach to the Santa Fe workshop, but our emphasis was decidedly on innovation and its role in the evolution of cultural systems. All 17 participants had extensive experience with

researching innovation and had made significant contributions to the literature on the subject. We assembled what we believe to be an impressive list of participants from a number of different disciplines—anthropology, archaeology, evolutionary biology, philosophy, and psychology. We asked the participants to prepare and circulate papers before arriving in Altenberg, which allowed us to move ahead with meaningful discussion once everyone was assembled. Additionally, we asked various individuals to concentrate on select aspects of innovation so that we achieved wider coverage than we might otherwise have gotten.

By all measures, the KLI workshop was a success—a point hopefully underscored by the content of the chapters included here. The book consists of a general introduction and three sections. The introduction documents the role that innovation has played in the explanation of cultural phenomena from roughly the late nineteenth century to the present. Ethnologists working early in the twentieth century paid particular attention to what typically were termed “culture traits,” using them as a means of linking related cultures together. Archaeologists did the same. Rarely, however, was there consensus on what a culture trait entailed and at what scale it should be examined. Beginning in the 1980s there occurred an emerging interest in applying evolutionary principles to the study of culture, and one area in which considerable advance was made was the study of cultural inheritance. As interesting and valuable as these studies are, there remain areas that need in-depth research, especially with respect to the production of cultural innovation and the scale and tempo at which it is produced.

Part II, “The Biological Substrate,” offers detailed discussions of innovation from several standpoints—epistemology (André Ariew), animal studies (Kevin Laland and Simon Reader), systematics and phylogeny (Jeffrey Schwartz), phenotypic plasticity and evolvability (Daniel Larson), and EvoDevo (Werner Callebaut). One thing becomes clear after reading the papers in this section: It no longer is sufficient to think of selection as “tinkering” with subtle variations, slowly effecting change over long periods of time. Rather, there are times when innovation appears as larger packages, the product of emergent human behaviors at fairly large scales.

Part III, “Cultural Inheritance,” documents the relevance of modern insights into innovation, including the simulation of cultural innovation in the laboratory (Joseph Henrich; Alex Mesoudi), the characterization of innovation using the random-copying (neutral) model (Alexander Bentley), the demographic analysis of culturally inherited skills (Adam Powell, Stephen Shennan, and Mark Thomas), evolutionary advantages of noninnovation (Craig Palmer), and variation in diffusion and rates of cultural change (Anne Kandler and James Steele).

Part IV, “Patterns in the Anthropological Record,” presents case studies that have examined cultural innovation in the archaeological and ethnographic records. Topics include technological innovation, developmental trajectories, and modes of social organization (Valentine Roux); the study of cultural variation from a behavioral perspective

(Michael Schiffer); and innovation as a social institution (Todd VanPool and Chet Savage).

We are extremely grateful to the KLI for funding the workshop. Our hosts—Gerd Müller, Werner Callebaut, Astrid Juette, and Eva Karner—went out of their way to make the event memorable. We also thank the fellows of the KLI, who added substantially to the discussions during and between sessions. Professor Müller, who along with Professor Callebaut is an editor for MIT Press’s *Vienna Series in Theoretical Biology*, guided us through the proposal process with the press. Finally, we thank Bob Prior, executive editor of MIT Press, for his unflagging support of the project, Susan Buckley, and Katherine Almeida, our editor. Melody Galen redrafted the figures into a common format, and Carla Schlink helped edit early versions of the chapters for consistency. Regina Gregory edited the final version.

9 Demography and Variation in the Accumulation of Culturally Inherited Skills

Adam Powell, Stephen J. Shennan, and Mark G. Thomas

In this chapter we introduce a simulation-based extension to an analytical model of cultural skill transmission presented by Henrich and Boyd (2002; Henrich 2004). Their original model derived the conditions necessary for a culturally inherited innovation, or cultural skill, to accumulate in a single population under a learning process that is both incomplete and inaccurate. Our simulation model extends these results by placing a modified version of their learning mechanism into a semirealistic human demographic setting with the aim of applying it in the context of the Upper Paleolithic transition. This was a pivotal period in human prehistory—the first sustained appearance of behavioral modernity—in which dramatic geographic and temporal variation in cultural innovation is evident. Although the invention of novel cultural skills or behaviors typical of the Upper Paleolithic is likely to have been stimulated by demographic pressures, cognitive advances, and environmental challenges, our simulation model is concerned solely with the long-term accumulation, or loss, of such cultural inventions. We propose that it is the maintenance, and not the invention, of novel traits that is of real interest and that this maintenance is limited by demographic factors. Our model is able to determine the demographic conditions necessary for a cultural skill to be maintained (or accumulate) over a period of many generations, and we argue that Late Pleistocene demography would have been an important factor in the appearance of the cumulative and complex cultural innovations characteristic of behavioral modernity.

The Upper Paleolithic transition, which occurred in Europe and western Asia ~45 thousand years ago (kya; Mellars 2005) and later in southern and eastern Asia (James and Petraglia 2005), Australia (Brumm and Moore 2005), and Africa (referred to as the Late Stone Age [Ambrose 1998a]), is seen by many as marking the origin of modern human behavior. This transition is characterized by a significant increase in both technological and cultural complexity, including the first consistent appearance of symbolic representation, and is often interpreted as evidence of the first “fully” modern human populations.

Bar-Yosef (2002) summarizes the main features characteristic of the Upper Paleolithic as follows:

- Rapid shifts in core-reduction techniques, leading to a proliferation of different micro-lithic stone tools, with blades largely replacing flakes.
- The use of bone, antler, and ivory in production of both functional tools and ritual artifacts.
- The systematic use of grinding/pounding stone tools to process plant food.
- Regular use of various body decorations from a wide variety of materials (including shells, teeth, ivory, and ostrich-egg shells), possibly signaling increasingly complex and/or frequent social interactions.
- The invention of improved hunting technology, such as spear throwers, bows, and boomerangs, potentially bringing much higher rates of hunting success.
- The appearance of art, both abstract and realistic, in the form of painting, engraving, and carved figurines.
- Unequivocal ritual burial, although there is also evidence of sporadic use of grave goods in Middle Paleolithic burials such as at Skhul V.
- A significant increase in the transfer distance of lithic and valuable raw materials.

In Europe and western Asia, this relatively rapid transition is widely thought to coincide with the expansion of *Homo sapiens* into a region previously occupied by Neanderthals (Bar-Yosef 2002; Zilhão 2007), leading to a period of coexistence of the two human lineages before the eventual extinction of the latter ~30 kya (Stiner and Kuhn 2006). For Africa, however, the idea of a short “seminal” transition has been contested by many authors, as there is evidence of many of these “markers of modernity” appearing at multiple sites across Africa well before 45 kya, possibly as early as 75–80 kya (Bar-Yosef 2002; Henshilwood et al. 2004; McBrearty and Brooks 2000), and most recently claimed for more than 160 kya in southern Africa (Marean et al. 2007). Yet these are sporadically maintained and are, in all cases, lost until the Late Stone Age, starting ~40 kya, when they again appear and become prevalent.

Archaeological evidence from South Asia and Australia appears more similar to the African case, with only sparse evidence of modernity—ornamentation, use of ochre, and possible rock art—occurring soon after the initial human expansions into the regions and becoming widespread only much later—~20 kya (Brumm and Moore 2005) in Australia and ~30 kya (James and Petraglia 2005) in southern Asia. Conversely, it has been argued that some late Neanderthal populations show features of behavioral modernity independent of any contact with modern humans (Conard 2005; Zilhão 2007).

Notwithstanding the oversimplifications made in the above outline, one important large-scale question remains: If, as is now widely accepted, anatomically modern humans (*H. sapiens*) originated in Africa between 150 kya and 200 kya (Lahr and Foley 1998; McBrearty and Brooks 2000; White et al. 2003), why was there such a long delay before

the first consistent archaeological evidence for modern human behavior? One approach (Klein 2000) is to argue that the transition, or “human revolution,” was a result of some kind of biological–neural mutation ~50 kya, which led to an increase in cognitive capacity, thus allowing an explosion of cultural and technological innovation.

Critics of this theory point to the low likelihood of this putative mutation having occurred independently in the many geographically separated human populations that would have existed at this time, given that there is no evidence for a second wave of Old World colonization by a group with such a mutation. Other authors (e.g., Lahr and Foley 1998; McBrearty and Brooks 2000) argue that the unambiguous evidence of modernity displayed in the African Middle Stone Age suggests that *H. sapiens* had the requisite cognitive capacity to be considered “fully modern” almost from the time of origin.

Some of the most notable examples of this African evidence associated with early modern humans are the (probably) hafted hunting weapons made of geometric blades of the Howiesons Poort industry in southern Africa (~55–70 kya; Lombard 2008), the series of barbed bone harpoon points at Katanda, Democratic Republic of the Congo (~90 kya; McBrearty and Brooks 2000), and the bone awls, pieces of ochre with abstract designs, and marine-shell personal ornaments at Blombos, South Africa (~74 kya; Zilhão 2007).

The arrival of anatomically modern humans in Australia (then part of the extended continent Sahul) dates to ~40–50 kya (Hudjashov et al. 2007; O’Connell and Allen 2004). Given that mastery of seaworthy technology would have been necessary to make the clearly intentional crossings of the Wallacean archipelago, a major ecological boundary, we can suggest that by that time *H. sapiens* had attained a modern level of cognition.

Numerous authors (Brumm and Moore 2005; James and Petraglia 2005; Lahr and Foley 1998; McBrearty and Brooks 2000; Shennan 2000, 2001; Zilhão 2007) view the emergence and consistent maintenance of modern cultural artifacts as a product of underlying demographic and associated sociological processes, although there are differences in the specific mechanisms invoked by different authors (see below). The basis of this view is the temporal correlation between the expansion and maintenance of modern human culture and the indication of major demographic expansion.

Our knowledge of late-Pleistocene demography remains extremely poor even in the best known regions of the world, but there is much evidence that populations were small in Africa and Eurasia until c. 50 kya, after which they are likely to have expanded rapidly. Stiner and Kuhn (2006) point to the narrow diet breadth and lack of impact on demographically sensitive small-game resources during the Middle Paleolithic in the circum-Mediterranean area as an indicator that population levels remained low. This is corroborated for some regions by site numbers (Lahr and Foley 2003; van Andel et al. 2003). Stiner and Kuhn (2006) propose that during the Middle Paleolithic, human populations responded to resource fluctuations by localized depopulation, and they suggest that human-population patterns corresponded to what we know about the population dynamics and low levels of large nonhuman predators.

Genetic evidence also points to marked increases in human populations in the late Pleistocene (Harpending et al. 1993; Rogers 1995; Sherry et al. 1994), and it has been argued that in Africa this expansion is associated with the improvement in climatic conditions associated with the end of Oxygen Isotope Stage 4 (Ambrose 1998b). The idea that there is a connection between demographic and cultural patterns and that both are affected by climate has been strengthened by recent work in Australia (Brumm and Moore 2005; O'Connell and Allen 2007), which seems to show a pattern similar to that seen in Africa but at a much later date. Thus, although Australia was colonized by modern humans ~40–45 kya, it shows only sporadic evidence of such phenomena as ornaments and burials for at least the next 20 millennia. It is only after 20 kya that they start to become more frequent and only in the early Holocene that they really become established, a pattern that seems to correlate with an order of magnitude increase in population size (Haberle and David 2004; O'Connell and Allen 2007). In this case, the improved climatic conditions of Holocene Australia are considered to be the most plausible causal factor (O'Connell and Allen 2007).

Models of the Relationship between Culture and Demography

Although many authors have postulated a link between the size of human populations and variation in the extent of cultural elaboration, the precise mechanism involved is unspecified in many, if not most, cases. However, three specific proposals have been made, none of them necessarily mutually exclusive. Several authors (O'Connell and Allen 2007; Stiner and Kuhn 2006; Vanhaeren 2005) propose that as populations increased, there would have been selective pressure for increasing use of various kinds of cultural-signaling mechanisms to strengthen social networks or to mark various kinds of identity, for example. In contrast, the two other models focus on processes of cultural transmission.

Some authors (e.g., Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981) have argued that human culture can be considered as an inheritance system, in some ways analogous to genetic inheritance, which is subject to evolutionary processes. They show that we can view human culture as a set of traits or behaviors that can be transmitted between individuals through a process of social learning, where “naive” copiers make inferences about the underlying behavior or trait based on its outward expression by a cultural model.

Of course, the mode of cultural transmission is different from that of genetic inheritance, as cultural traits can be transmitted not only from genetic parent to child (vertical transmission) but also from nonparental members of a group (oblique transmission) and between peers (horizontal transmission). Variation in these cultural traits is generated either at the learning stage, through mistakes in the inferential process (random copying error), by

deliberate innovation, or by combining the traits of multiple cultural models, when the trait is expressed by the copier (a cognitive process).

An important component required of any evolutionary system is that of the differential success of variants in a population; in the case of cultural evolution this is driven by a number of mechanisms. These “forces of cultural evolution” (Boyd and Richerson 1985) include “cultural drift,” which causes fluctuations in cultural-variant frequencies over time due to sampling error in populations of finite size; “guided variation,” in which individuals modify their socially learned cultural variants through their own process of trial and error; and “biased transmission,” where learners adopt a cultural variant preferentially (nonrandomly) as a result of (1) some intrinsic quality of the trait, (2) behavior itself (“directly biased transmission”), (3) a perceived quality of the cultural model that possesses it (“indirectly biased transmission”), or (4) the relative frequency of the variant in the population (“frequency-dependent biased transmission”). Thus, change over time in the frequencies of different cultural variants and their subsequent material expression in the archaeological record can be viewed as a result of these various processes of cultural evolution acting on socially learned traits, skills, or behaviors.

A review of the ethnographic literature (Shennan and Steele 1999) on the learning of craft skills shows that transmission in hunter–gatherer populations is almost exclusively vertical/oblique and is in many cases between parent and offspring of the same gender. This finding is consistent with the results of a model-based treatment of African cultural variation (Guglielmino et al. 1995), which found that the more conservative modes of cultural transmission (vertical/oblique) best explain the distribution of variation observed. It seems reasonable to assume that the mode of transmission of cultural skills within Late Pleistocene human populations would have been comparable to these contemporary hunter–gatherer groups.

In Shennan’s (2001) simulation model based on Peck (1996; Peck et al. 1997), the mechanism that linked population size and variation in (beneficial) cultural accumulation was drift. It was shown that when cultural-innovation processes take place and the results are passed on by a combination of vertical and oblique transmission, larger populations have a major advantage over smaller ones. Members of larger populations are, on average, both biologically more fit and more attractive as models for imitation by virtue of the fact that the deleterious sampling effects present in small populations decline as population sizes increase. When populations are small, innovations that are less beneficial reproductively and less attractive to imitate are more likely to be maintained within them, that is, they have a greater “drift load.”

A different transmission model, one based on the varying difficulty of learning different skills and the associated probability of achieving an improvement, was proposed by Henrich and Boyd (2002) and applied to explain the well-known pattern of cultural loss in Holocene Tasmania (Henrich 2004). This analytical model showed that under certain conditions, dependent on the population size (discussed below), the “cumulative

adaptive evolution” of a cultural skill can occur, whereas in other circumstances a process of devolution and cultural loss will follow. Here we extend this model by using semirealistic stochastic simulations that reflect plausible human demographic conditions during the Pleistocene and take into account some of the drift issues highlighted in Shennan (2001).

The Henrich and Boyd Model

The model assumes a population of N adults, that is, “encultured” individuals, $i = 1, 2, \dots, N$, each of which has a z value, z_i , a measure of its ability at some cultural skill, such as making arrowheads. Every adult individual is also characterized by a variable, f , that specifies the relative likelihood of being chosen as a cultural model by members of a subsequent generation. The authors (see Henrich [2004] for full details) make use of the Price equation, a means of delineating the processes at work within any evolutionary system (Frank 1995; Price 1970), to measure $\Delta\bar{z}$, the change in the average z value in the population over time:

$$\Delta\bar{z} = Cov(f_i, z_i) + E(f_i \Delta z_i) \quad (9.1)$$

The two terms on the right-hand side can be thought of, respectively, as the change in the average z value resulting from cultural selection, that is, the propensity to copy successful or skilled people, and the change resulting from the inaccurate transmission process. Where $\Delta\bar{z}$ is positive, “cumulative adaptive evolution” is occurring, with the average ability at the cultural skill increasing over time within the modeled population. In order to replicate the “incomplete and inaccurate” processes of inference, copiers in subsequent generations never exactly replicate the z value of their models. An individual attempting to copy a model with z value z_i gains a value drawn from a Gumbel distribution (Henrich [2004] notes that the specific form of distribution does not qualitatively affect any derived results) with mode $(z_i - \alpha)$ and dispersion parameter β , meaning that the transmission process is, first, systematically biased, as, on average, a copier will end up with a z value less than that of his or her model by an amount α , and, second, “noisy,” so that there is a small probability (the area under the distribution greater than the model’s z value), monotonically related to β and inversely related to α , that copiers will gain a z value greater than that of their model.

The model stipulates that all social learners choose the most-skilled member of the previous generation as their oblique model, and the following equation is derived:

$$\Delta\bar{z} = -\alpha + \beta(\varepsilon + \ln(N)) \quad (9.2)$$

The first term on the right represents the deleterious effect of systematic bias, and the second describes the opposing, favorable effect of random noise (ε being the Euler-gamma constant ≈ 0.577) and is a proxy measure of the area of the distribution greater than the

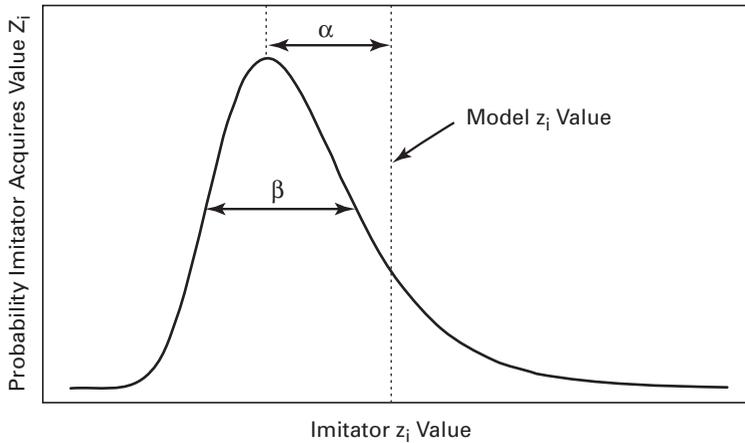


Figure 9.1
Gumbel distribution for incomplete and inaccurate transmission process.

model z value (see figure 9.1). To find the conditions under which cultural transmission will result in adaptive accumulation, the authors set $\Delta\bar{z} > 0$ and rearrange (9.2) to get

$$N^* > e^{\frac{\alpha}{\beta} - \epsilon} \quad (9.3)$$

where N^* is the critical number of social learners necessary for a specific process of imitation defined by (α, β) . (See figure 9.2.)

The main conclusion of interest here is that the cumulative adaptive evolution of a culturally inherited skill is dependent on the size of the pool of social learners N , so a larger population (subject to the same level of noise in the imitation process) would be able to accumulate and maintain a more “complex” skill. As the critical conditions for adaptive evolution depend solely on the ratio α/β , and if we assume that all modern human populations, on average, would have been subject to similar levels of random noise during the inheritance of cultural skills, we can effectively combine the two parameters α and β by setting $\beta = 1$ and then simply adjusting the parameter α to simulate cultural skills of varying “complexity.”

One assumption inherent in the model is the unfailing ability of naive individuals to accurately identify the most skilled member of the preceding generation as an oblique model—an assumption that rapidly becomes unrealistic as the size of the adult population increases beyond the size of a sustainable social network. By imbedding an extended version of the transmission process previously described (to include both vertical and oblique transmission) into a semirealistic simulation that estimates conditions during the Late Pleistocene—that is, a number of geographically separate subpopulations connected

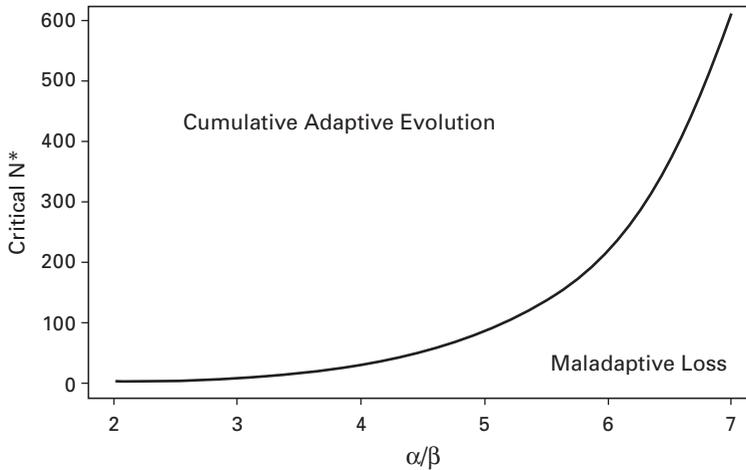


Figure 9.2

The conditions necessary for cumulative adaptive evolution.

by migratory activity—we can relax this assumption and further investigate the effects of early human demography on the accumulation of cultural skills. In the following sections we introduce and detail the simulation model, present the main theoretical results, and discuss their possible implications in future debate on the nature and causes of the appearance and accumulation of modern human culture.

Model 1: Extending the Analytical Model

Our underlying simulation model consists of a number of subpopulations, G , placed at random in a two-dimensional simulated world. Each subpopulation contains N adult individuals, and all subpopulations are connected by migratory activity. In every generation of the simulation, the model goes through the following steps:

1. Within each subpopulation a generation of offspring, also of size N , is created.
2. Genetic parents are chosen for each offspring by randomly sampling the adult generation with replacement.
3. Naive offspring then undergo a process of “vertical transmission,” where they receive a z value by learning from their genetic parents according to the transmission process described by Henrich and Boyd (2002) and detailed above.
4. A proportion, P_{ob} , of these offspring then undergoes a process of “oblique transmission,” where they replace their z value with one learned from the maximally skilled member of the adult generation in the subpopulation (the *oblique model*).

5. The now-“encultured” offspring generation then fully replaces the adult generation within each subpopulation.
6. A proportion, P_{mig} , of these new adults then migrates, with each migrant being placed in a new subpopulation by a Gaussian random-walk-like process.

Each simulation is initialized by giving all individuals in all subpopulations a z value of 10.0, then running forward for 50 generations, and after the final generation, calculating the world mean z value. This value is compared to the starting world mean (10.0) to determine whether this simulation results in “adaptive cumulative evolution,” i.e., $\Delta\bar{z} > 0$. To account for stochastic variation in simulation outcomes, we perform multiple iterations, making this calculation at the end of each iteration. We then calculate the mean z value across iterations and deem the parameter set to be “cumulatively adaptive” if it is greater than the mean starting z value, i.e., >10.0 .

We recognize that the time spans we are considering are 10,000–20,000 years (around 400–800 generations), but preliminary tests showed that 50 generations was in most cases sufficient to determine whether the parameter set would result in cumulative adaptive evolution or maladaptive loss—with mean z values either increasing monotonically without bound, decreasing monotonically to zero (at which point the cultural skill is irretrievably lost), or reaching a relatively stable equilibrium value. The model is also relatively conservative, in that it currently disregards the likely autocatalytic/positive feedback loop, where increasing ability in some cultural skills would lead to improved demographic conditions (by means of improved reproductive success/resource utility), which would, in turn, further increase skill accumulation.

The parameters of interest in this model are the number of subpopulations, G ; the size of each subpopulation, N ; the proportion of offspring to undergo oblique transmission, P_{ob} ; the proportion of each subpopulation available to migrate, P_{mig} ; and the “complexity” of the skill, α . Because of the difficulty in accurately estimating demographic parameters during the Pleistocene, we turn to a review of contemporary Australian aboriginal hunter-gatherer populations (Birdsell 1973) to draw some estimates for N . Two regularly occurring distinct social structures of differing size are identified. The first is the “band,” an independent and autonomous patrilineal unit commonly comprising 25–50 individuals (usually an extended familial group), and the second, the “tribe,” comprising around 500 or so individuals related by linguistic or dialectal similarity and forming a generally endogamous unit.

To complement these two contemporary ethnographic estimates, there are also analyses emerging from biological anthropology (Dunbar 1992, 1993) that may shed light on the question of early human subpopulation sizes. Dunbar argues that social-group size in primates is likely to reflect the cognitive capacities of the individuals comprising it, as there is thought to be a cognitive upper limit on the number of social interactions that can be maintained and thus a limit on group size. Extrapolating a relationship between

neocortex ratio and social-group size in nonhuman primates to humans gives a prediction for ancestral group size in the region of ~ 150 .

We need to bear in mind that the value of N in our simulation refers to the total number of social learners in the offspring generation and that, as we are assuming that 50 percent of each group is subadult and that a cultural skill is inherited by same-sex offspring, this represents roughly a quarter of each actual subpopulation size. Based on the previous estimates, we have simulated over values of N between 5 and 100, corresponding to total group sizes of ~ 20 –400, recognizing that actual Pleistocene group sizes are likely to have been weighted toward the lower end of this range.

In estimating the migration rate, P_{mig} , we make use of an earlier Birdsell (1968) study giving an aboriginal intertribal marriage rate of ~ 15.7 percent, which corresponds to a migration rate of around 0.074. This is consistent with another Australian aboriginal study that yielded estimates of between 0.07 and 0.21 (Tindale 1953; see Eller et al. 2004). Even if Pleistocene subpopulations were comparable in size to contemporary hunter-gatherer groups, it is likely that subpopulation densities and intergroup interactions prior to the emergence of Late Stone Age/Upper Paleolithic technology were significantly lower than the contemporary estimates for migration rates. We therefore simulated over a range of migration rates, P_{mig} , between 0.001 and 0.15.

Although oblique transmission, and prestige-biased transmission in particular (Henrich and Gil-White 2001), is undoubtedly important in the transmission of cultural skills (Guglielmino et al. 1995; Shennan and Steele 1999), it is difficult to make realistic estimates of the extent to which it occurred. For this reason, we have simulated P_{ob} over the entire range of 0.1 to 1.0 (in increments of 0.1). The number of subpopulations, G , likely was subject to significant fluctuations during the Pleistocene, for reasons outlined above, so we simulated for a wide range of G , from 1 up to 500.

Preliminary simulation results indicate that as G increases beyond ~ 100 , there is only a small increase in mean z value, suggesting that a “saturation point” is reached with regard to skill accumulation. Given this, and making the reasonable assumption that the number of interconnected human subpopulations during the Middle Stone Age was likely to have been at least this large, we fix $G = 100$ in future simulations. These simulations also showed that adjusting the value of N has no qualitative effect on the results, so fixing $N = 25$ from here on entails no loss of generality.

Simulation results are presented in figures 9.3 and 9.4 and show that the degree of skill accumulation increases with increasing oblique transmission probability (see figure 9.3), increasing migration rate (see figure 9.4), and decreasing complexity (as measured by the α value). The shaded regions give the parameter sets that result in cumulative adaptive evolution, i.e., mean final z value > 10.0 .

This model defines the migration rate at the global level (P_{mig}), operating for all subpopulations irrespective of the local subpopulation density. As a result, it is impossible to ascertain the effects of having different subpopulation densities in different regions of the

Model 1

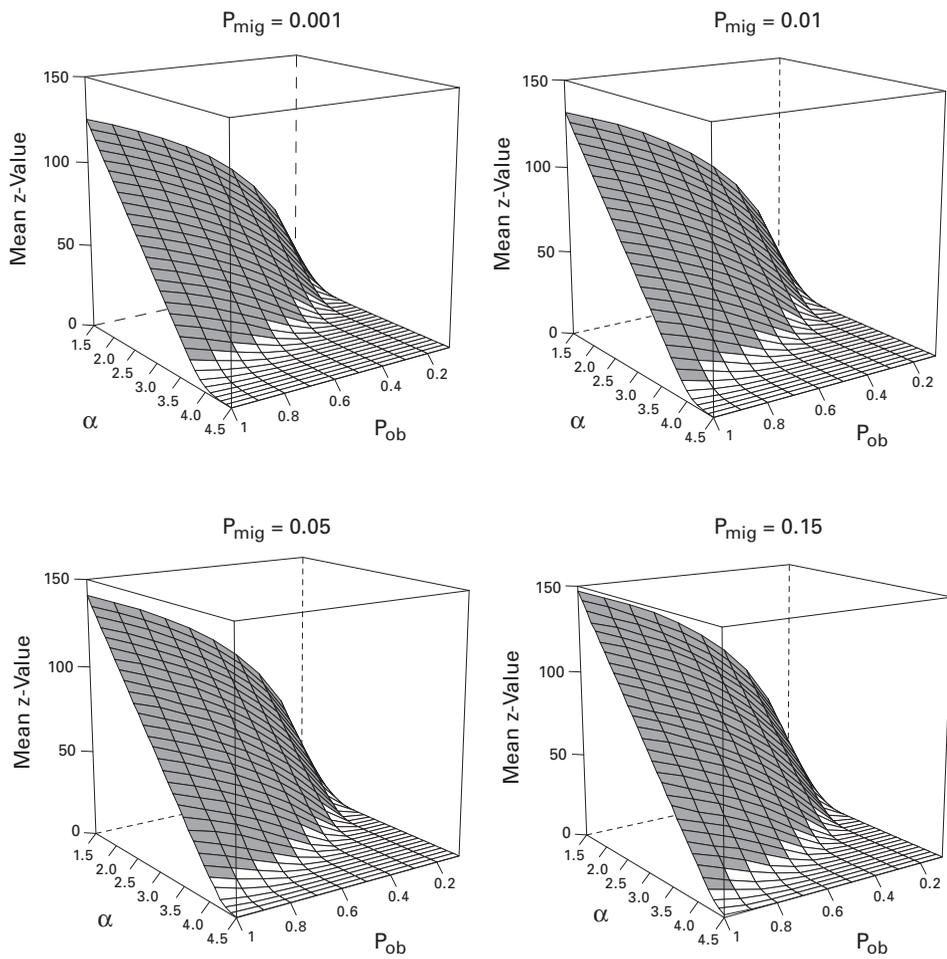
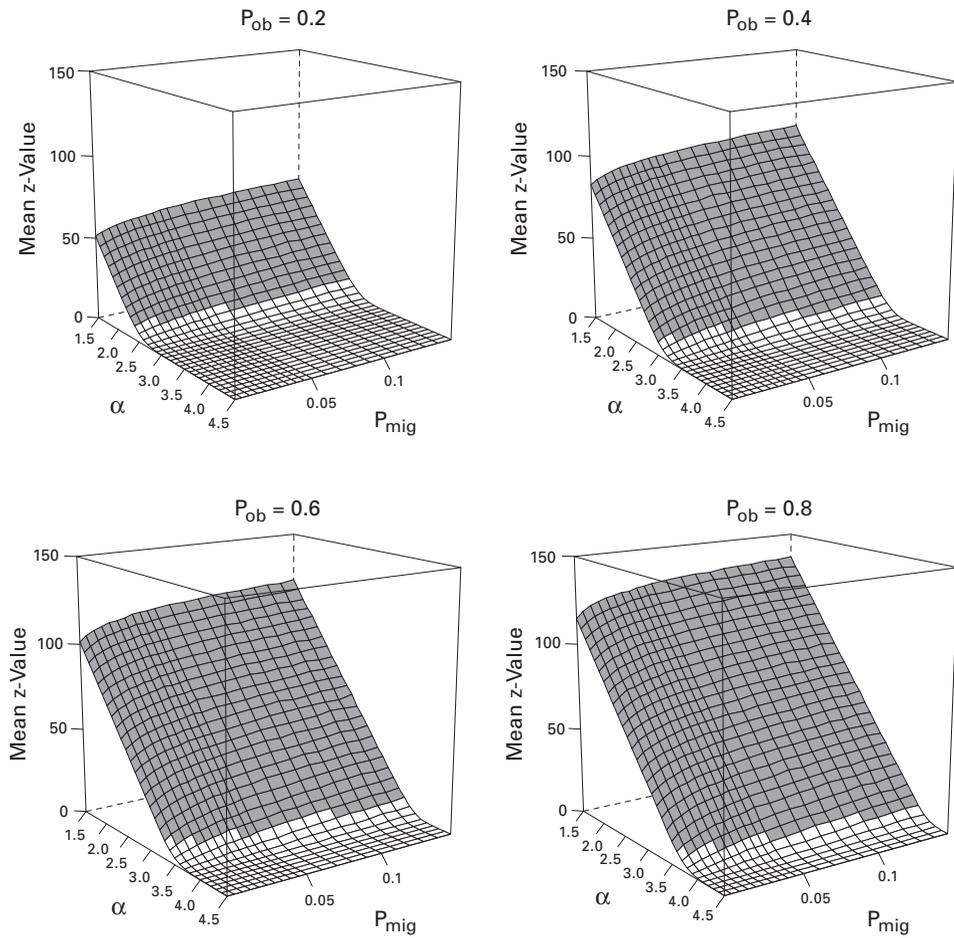


Figure 9.3 Model 1 simulation results, showing mean z values for combinations of parameters α and P_{ob} (oblique-transmission probability), given for four different migration rates (P_{mig}). Shaded regions indicate parameter sets resulting in cumulative adaptive evolution, that is, mean z value > 10.0 .

Model 1

**Figure 9.4**

Model 1 simulation results, showing mean z values for combinations of parameters α and P_{mig} (migration rate) given for four different oblique-transmission probabilities (P_{ob}). Shaded regions indicate parameter sets resulting in cumulative adaptive evolution, that is, mean z value > 10.0 .

same simulation world. A far more realistic model would explicitly link local migration rates to local subpopulation density. To this end, we have added an extra level of complexity to our simulation model as detailed below.

Model 2: Subpopulation Density–Dependent Migration

The migration process in this model is now explicitly dependent on subpopulation density. We define the global density of subpopulations, D , and adjust the dimensions of the simulation world so that we get ~ 100 subpopulations, a value for G we showed above to be reasonable. The model then creates a simulation world by placing, again at random, the subpopulations. At the migration step in the simulation, all adult individuals now undergo a Gaussian random-walk process, with the standard deviation of the Gaussian distribution defined by a new parameter, M_{sd} . The adult individuals that “hit” any other subgroup during this process are deemed to move to that group; otherwise, they are deemed not to migrate and to remain in their original subpopulation.

The parameter M_{sd} , which can be thought of as the “migratory range” of an individual, is defined as a proportion of the average nearest neighbor distance, \bar{r}_E , between subgroups within the simulation world. A derivation presented by Clark and Evans (1954) gives this average nearest neighbor distance between randomly distributed subpopulations in terms of density as

$$\bar{r}_E = \frac{1}{2\sqrt{D}},$$

which is shown in figure 9.5.

If we note that around 99.7 percent of the probability density of a Gaussian distribution lies within ± 3 standard deviations, we would expect that when $M_{sd} \leq 1/3$ many subpopulations would be effectively isolated from all others as migrants would be unable to reach them; therefore, their internal skill accumulation would be unaffected by the migration process. Test simulations—where we calculated the mean global migration rate—confirmed this and showed that for M_{sd} greater than ~ 0.3 , the mean global migration rate approximately equals the global subpopulation density, D (see figure 9.6).

For our current purposes, we set M_{sd} well above this critical value at 1.0, that is, equal to \bar{r}_E , so we can be sure that few subpopulations are completely isolated and that the mean global migration rate, and thus the effect on the accumulation of cultural skills, will depend solely on the underlying global subpopulation density. We simulate for 50 generations, over a range of α values and again for the entire range for P_{ob} (0.1–1.0).

Simulation results for this model show (in broad agreement with model 1 results) that skill accumulation increases with increasing oblique-transmission probability (see figure 9.7), with increasing subpopulation density (see figure 9.8), and with decreasing complexity (as measured by the α value).

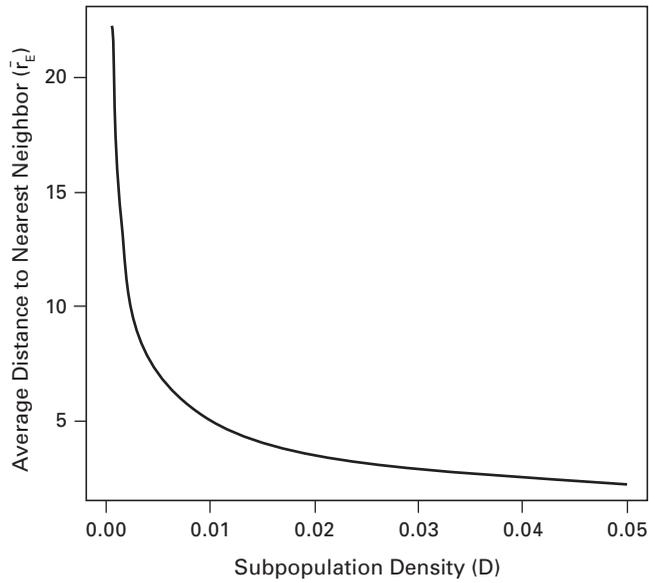


Figure 9.5

Average nearest neighbor distance between randomly distributed subpopulations.

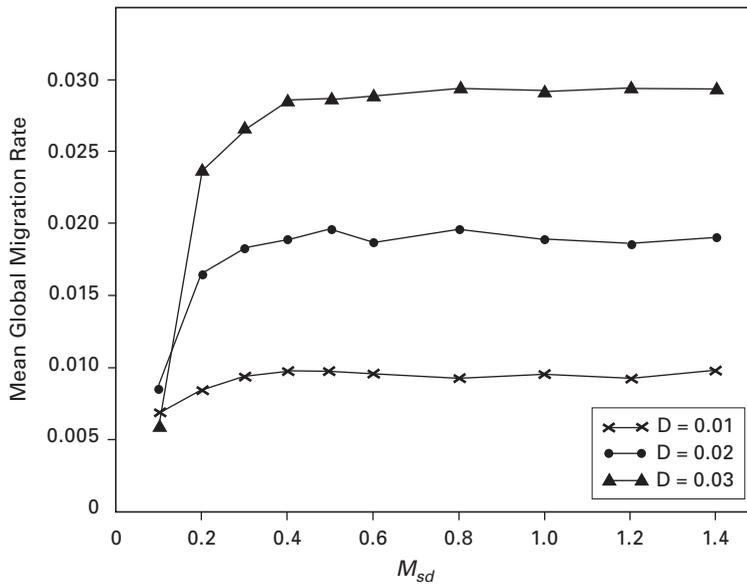


Figure 9.6

Mean global migration rate for increasing M_{sd} (migratory range) from test simulations. D = subpopulation density.

Model 2

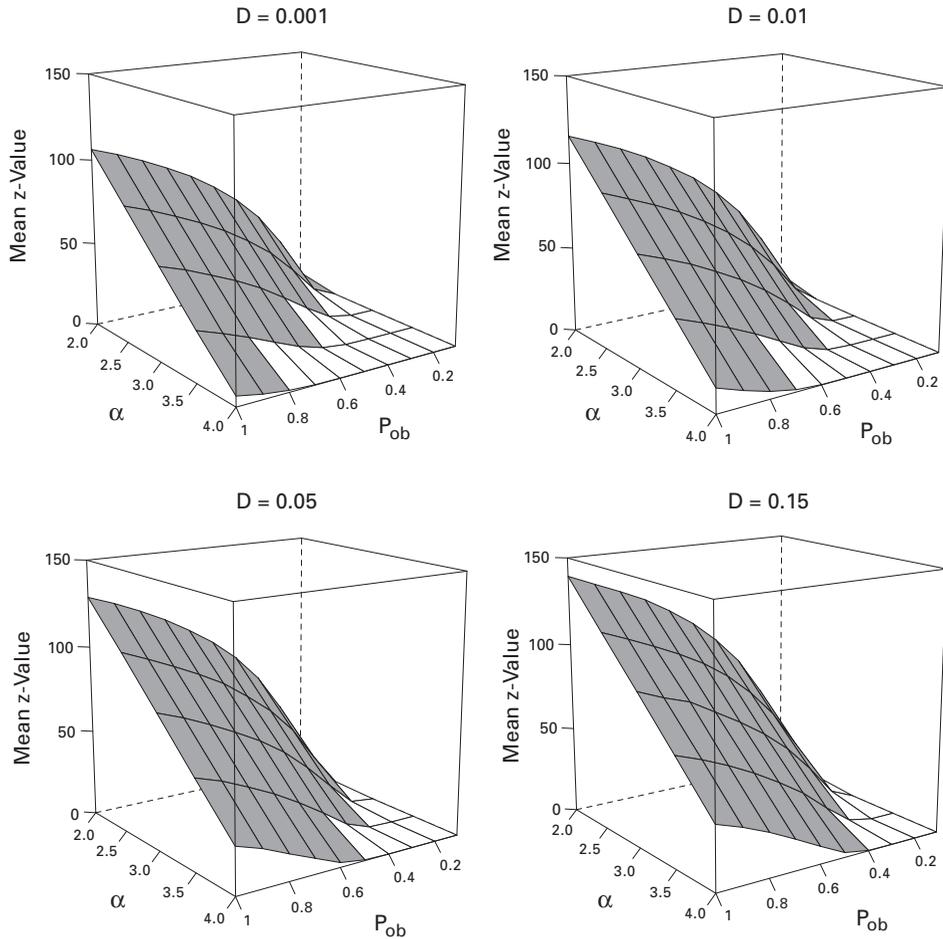
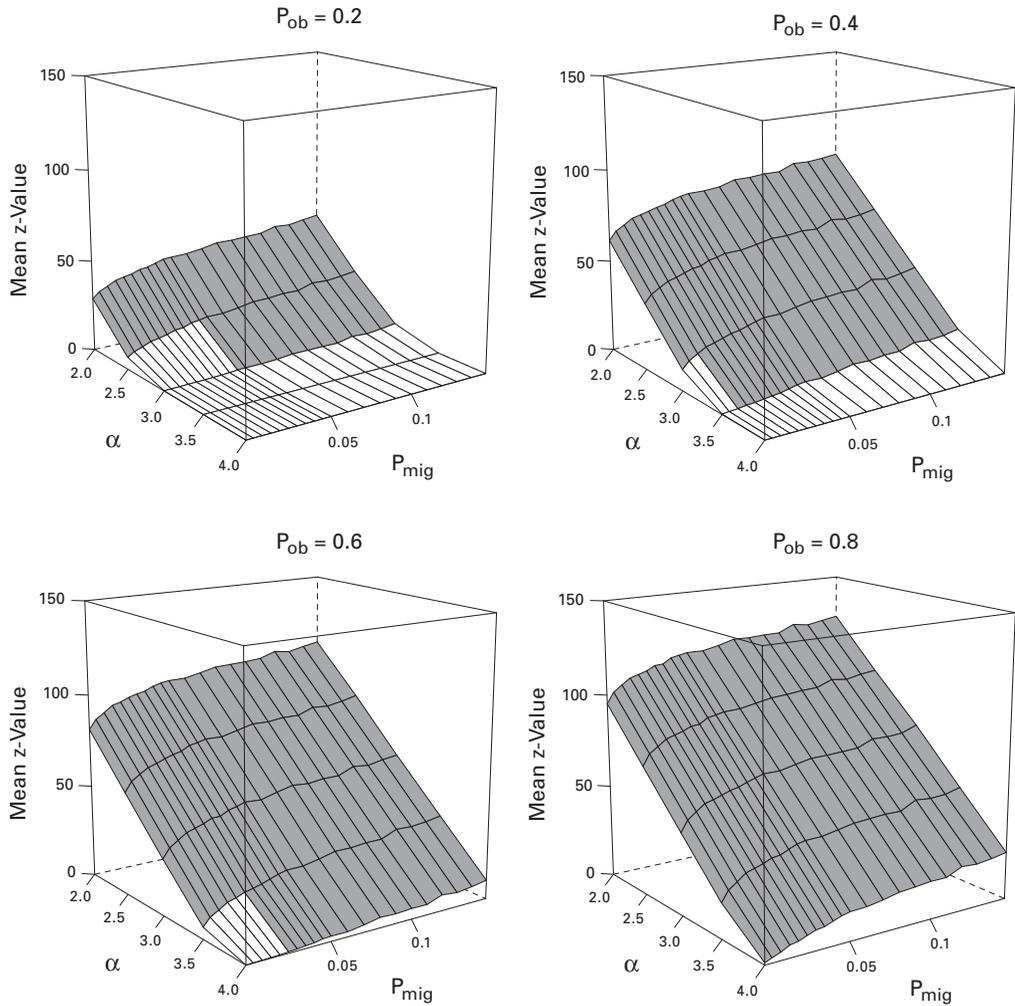


Figure 9.7

Model 2 simulation results, showing mean z values for combinations of parameters α and P_{ob} (oblique-transmission probability), given for four different subpopulation density (D) values. Shaded regions indicate parameter sets resulting in cumulative adaptive evolution, that is, mean z value > 10.0 .

Model 2

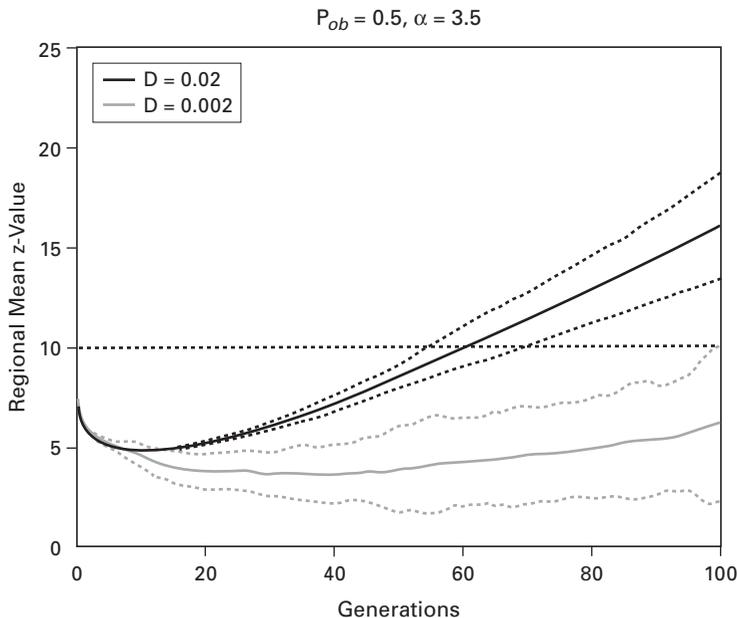
**Figure 9.8**

Model 2 simulation results, showing mean z values for combinations of parameters α and D (subpopulation density) given for four different oblique-transmission probabilities (P_{ob}). Shaded regions indicate parameter sets resulting in cumulative adaptive evolution, that is, mean z value > 10.0 . P_{mig} = migration rate.

Model 2.1: Heterogeneous Subpopulation Density

A minor adjustment to the previous model allows us to investigate the effect of dividing the simulation world into two regions of different subpopulation densities. We partition the simulation world in half along the east–west axis and populate one half at a subpopulation density D_{high} and the other at a density an order of magnitude lower, D_{low} . In the following simulations, we set $M_{sd} = 1.0$ as a proportion of the average nearest neighbor distance, \bar{r}_E , in the lower density region, again to ensure that all subpopulations are connected by migration (including across the density divide). We set $D_{high} = 0.02$ and $D_{low} = 0.002$ and the dimensions of the world at 100×100 , giving us a total of 110 subgroups, and simulate for a range of α values (2.0–4.0) and for values of P_{ob} (0.25, 0.5, 0.75, and 1.0) over 100 generations, performing 100 iterations for each.

In these simulations (data not shown), we find that skill accumulation is consistently higher in the higher-density region. As an example, we can fix $\alpha = 3.5$ and $P_{ob} = 0.5$ and look at the average z values in each region over time. Figure 9.9 shows that this difference is maintained over the entire (extended) duration of the simulation. The 95 percent confidence intervals, as estimated by taking mean regional z values for 100 iterations, show

**Figure 9.9**

Example simulation result from model 2.1 (oblique-transmission probability [P_{ob}] = 0.5, $\alpha = 3.5$) with heterogeneous subpopulation density (D). Solid lines give the mean z value in each region; dotted lines give the 95 percent confidence intervals (from 100 iterations).

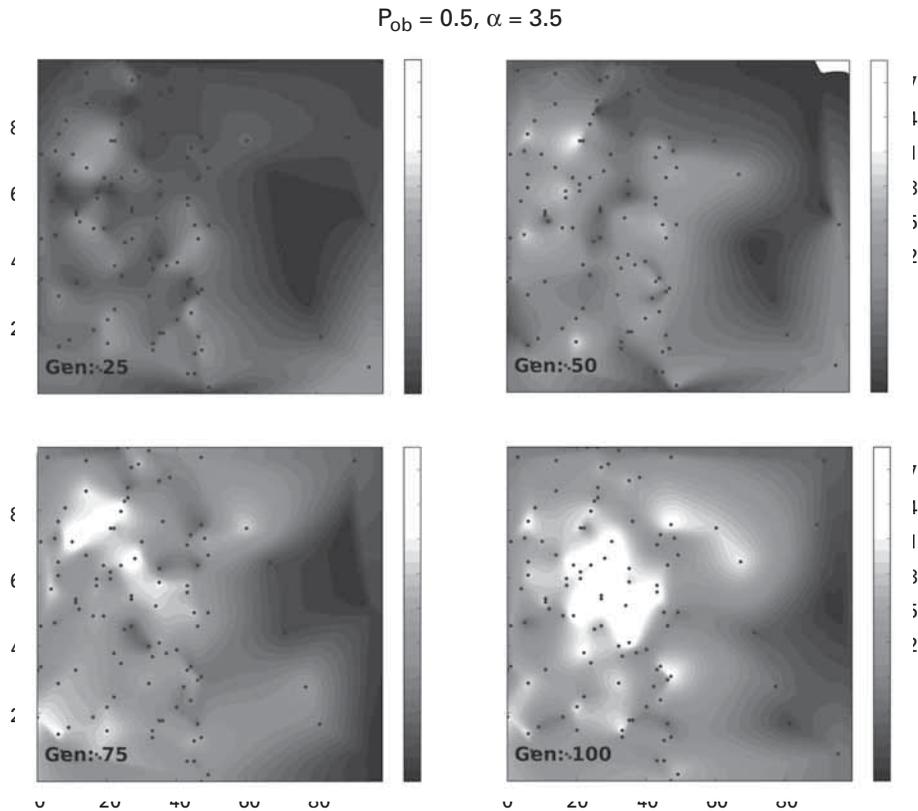


Figure 9.10

Spatial structuring of skill accumulation (model 2.1 example result) taken at 25-generation intervals. Subpopulations are shown as black points; mean z values are surface interpolated.

that the difference in accumulated z values between the different density regions becomes significant after less than 20 generations.

A visual illustration of this spatial structuring of skill accumulation can be seen in figure 9.10. In this example, a series of “snapshots” of a single iteration are taken at 25-generation intervals, and the subpopulation z values are surface interpolated to show “spatial skill accumulation.”

Model 2.2: Heterogeneous Migratory Range

A further modification of the model allows us to divide the world into two regions of identical population density but differing migratory range, M_{sd} . This allows us to explore the effect of reduced migratory range on the accumulation of cultural skills in geographic space. We set $M_{sd,high}$ at 1.0 and $M_{sd,low}$ an order of magnitude lower, at 0.1. Figure 9.11

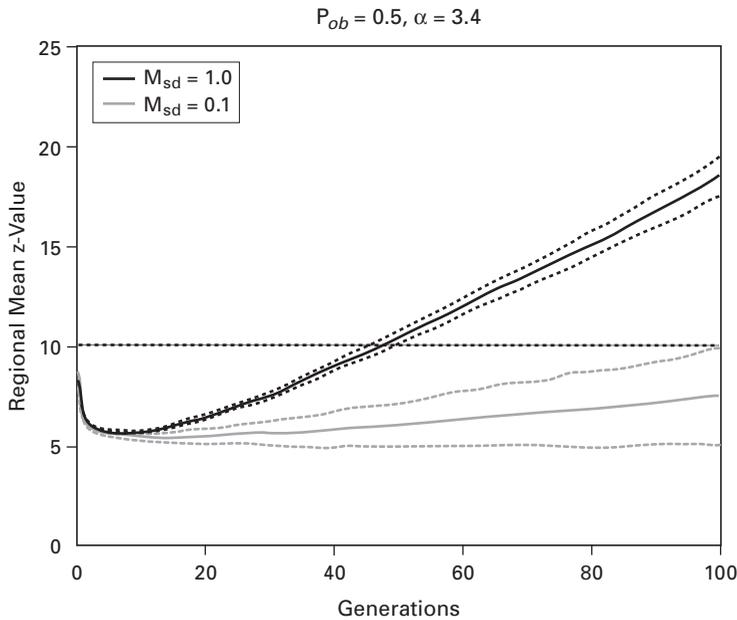


Figure 9.11

Example simulation result from model 2.2 (oblique-transmission probability [P_{ob}] = 0.5, $\alpha = 3.4$) with heterogeneous migratory range (M_{sd}). Solid lines give the mean z value in each region; dotted lines give the 95 percent confidence intervals (from 100 iterations).

shows the results for $D = 0.01$, $\alpha = 3.4$, and $P_{ob} = 0.5$ across 100 generations and using 100 iterations to estimate the 95 percent confidence interval of z values for each region. As with the heterogeneous density simulations, we can see that the regional mean z value becomes significantly higher in the high migratory-range region after less than 20 generations. A surface-interpolation plot illustrating this spatial structuring of skill accumulation over time is presented in figure 9.12.

“Natural” Oblique-Transmission Methods

In all previous models, we parameterized the proportion of offspring undergoing oblique transmission (P_{ob}), which, as discussed above, is difficult to estimate from the ethnographic record. The identification of the oblique model was also assumed to be perfectly accurate, which ignores the likely difficulty of this process in the real world, even within the much smaller subpopulations we have modeled. To avoid these difficulties and to reduce the number of parameters in the model, we have developed a number of more “natural” processes for oblique transmission, which we surmise may more realistically reflect processes by which oblique models are chosen within human populations. Under these new methods, all offspring identify and select an oblique model with a degree of uncertainty and replace

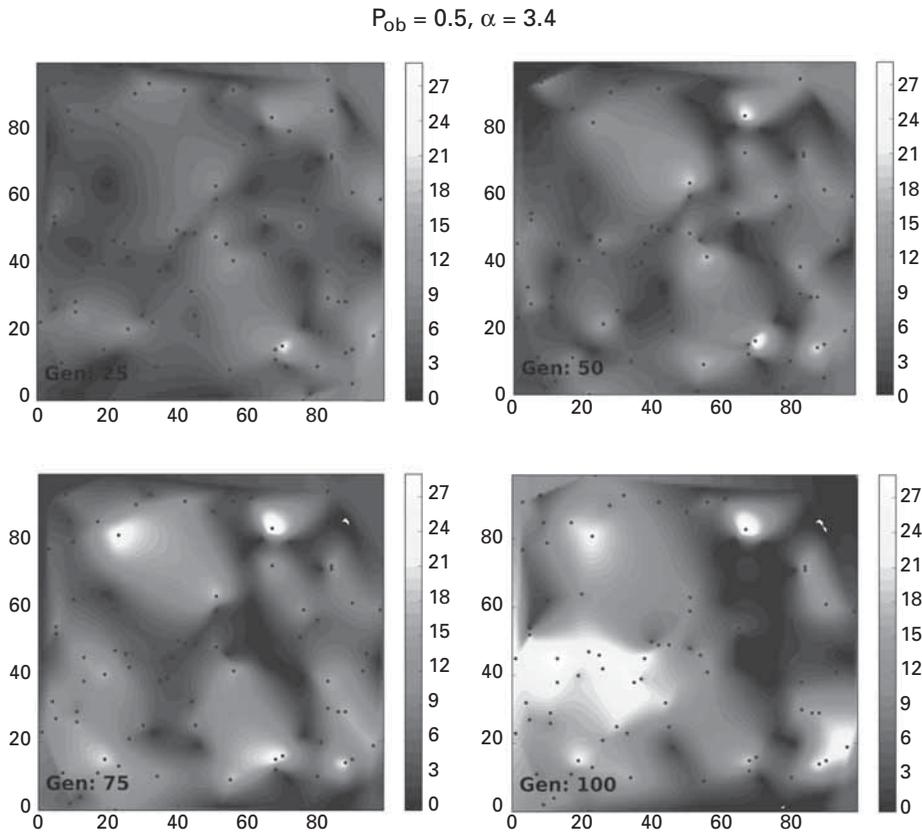


Figure 9.12

Spatial structuring of skill accumulation (model 2.2 example result) taken at 25-generation intervals. Subpopulations are shown as black points; mean z values are surface interpolated.

their current z value, that is, the one gained vertically from a parent, only if the value they gain from their chosen oblique model is greater.

In method 1, each offspring selects an oblique model from the adult generation, with probability proportional to the squared adult z value. In method 2, each offspring selects an oblique model from among only the adults with z values greater than what was already gained from a biological parent, with probability proportional to the magnitude of the difference. In method 3, each offspring selects an oblique model from the adult generation, with probability proportional to the difference between each adult's z value and the minimum adult z value in the subpopulation.

All simulations were run in a homogeneous simulation world, that is, where $M_{sd} = 1.0$ and with D kept constant both across the whole world and with each of the three alternative processes, so results can be compared, possibly allowing us to identify an efficient

(or near-optimal), realistic cultural-learning strategy. We simulated for 50 generations, performing 100 iterations, for a range of subpopulation densities, D , and skill complexities, α , for each of the three “natural” oblique methods.

Results for the three methods again show the general result that increasing subpopulation density and decreasing skill complexity, α , leads to increased skill accumulation (see figure 9.13). Method 2 consistently results in greater mean z values, thus leading to cumulative adaptive evolution (the shaded regions), even for more complex skills and at lower subpopulation densities than either of the other two methods.

Discussion

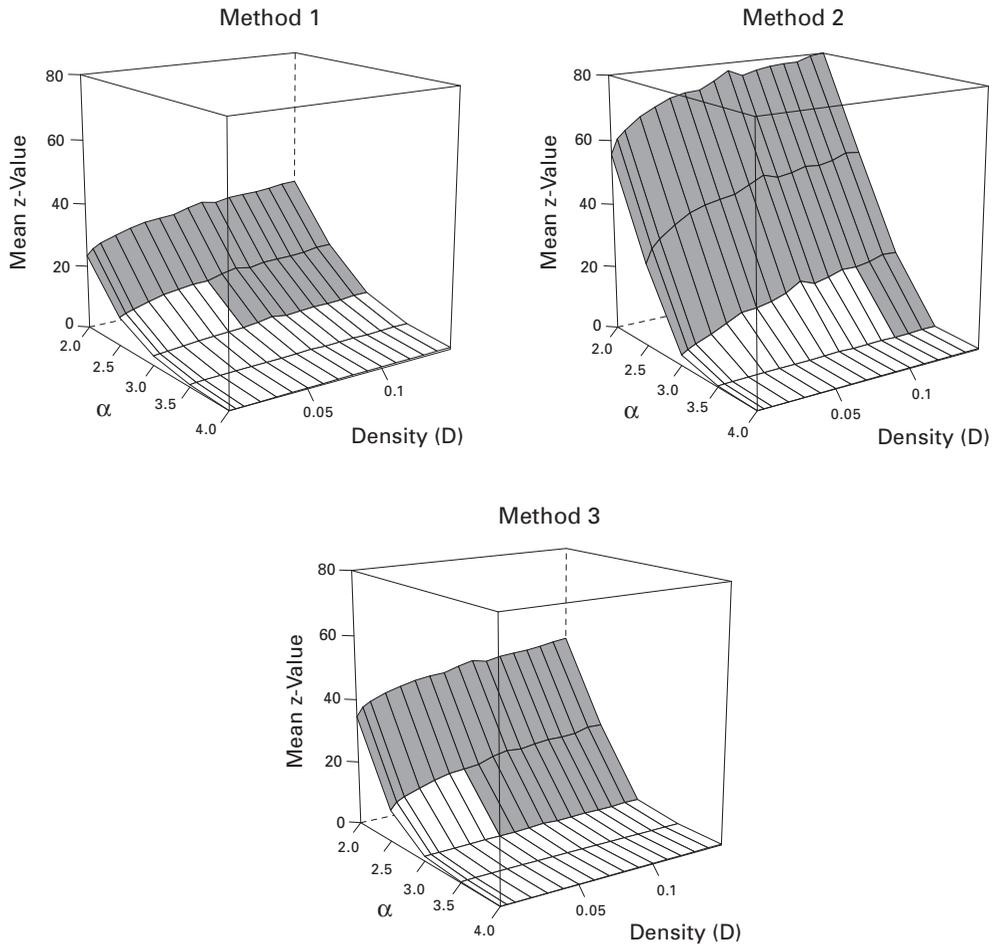
Our results show that the level of cultural skill that can be maintained in subpopulations is related to the density/migratory activity of those subpopulations. In cases where densities/migration rates are low, cumulative adaptive evolution will never occur. Even in cases with higher densities and migration rates where it does occur, there is a significant period before accumulation begins, with potential consequences for population viability.

We also demonstrate that geographic heterogeneity in local subpopulation density/migratory activity leads to stable spatial structuring of skill accumulation, so that areas where skills accumulate can exist contiguously with areas of skill devolution over long periods of time.

The last set of simulations presented compared different “natural” strategies of choosing an oblique model within subpopulations, which recognize that individuals will not always be in a position to identify the individual with the maximum skill level. Results show that method 2—in which each offspring selects an oblique model from among only the adults with z values greater than what the offspring has already gained from a biological parent, with probability proportional to the magnitude of the difference—leads to cumulative adaptive evolution for more complex skills (characterized by a higher α value) and at lower densities than possible alternatives.

These results confirm and extend Henrich’s (2004) initial results and show that the action of demographic factors on the results of cultural-transmission processes using plausible parameter values could indeed have had the effect on cumulative adaptive evolution that many others have postulated as central to the slow pace of cumulative cultural evolution prior to c. 50 kya and its greatly increased speed thereafter.

"Natural" Oblique Methods

**Figure 9.13**

Simulation results for the three natural oblique-transmission methods, showing mean z values for combinations of parameters α and D (subpopulation density). Shaded regions indicate parameter sets resulting in cumulative adaptive evolution, that is, mean z value > 10.0 .

References

- Ambrose, S. H. 1998a. Chronology of the Later Stone Age and Food Production in East Africa. *Journal of Archaeological Science* 25: 377–392.
- Ambrose, S. H. 1998b. Late Pleistocene Human Population Bottlenecks, Volcanic Winter, and Differentiation of Modern Humans. *Journal of Human Evolution* 34: 623–651.
- Bar-Yosef, O. 2002. The Upper Paleolithic Revolution. *Annual Review of Anthropology* 31: 363–393.
- Birdsell, J. B. 1968. Some Predictions for the Pleistocene Based on Equilibrium Systems among Recent Hunter–Gatherers. In *Man the Hunter*, edited by R. B. Lee and I. DeVore, pp. 245–248. Aldine, Chicago.
- Birdsell, J. B. 1973. A Basic Demographic Unit. *Current Anthropology* 14: 337–356.
- Boyd, R., and P. J. Richerson. 1985. *Culture and the Evolutionary Process*. University of Chicago Press, Chicago.
- Brumm, A., and M. W. Moore. 2005. Symbolic Revolutions and the Australian Archaeological Record. *Cambridge Archaeological Journal* 15: 157–175.
- Cavalli-Sforza, L. L., and M. W. Feldman. 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton University Press, Princeton, N.J.
- Clark, P. J., and F. C. Evans. 1954. Distance to Nearest Neighbor as a Measure of Spatial Relationships in Populations. *Ecology* 35: 445–453.
- Conard, N. 2005. An Overview of the Patterns of Behavioural Change in Africa and Eurasia during the Middle and Late Pleistocene. In *Tools to Symbols from Early Hominids to Humans*, edited by F. d’Errico and L. Blackwell, pp. 294–332. Wits University Press, Johannesburg.
- Dunbar, R. 1992. Neocortex Size as a Constraint on Group Size in Primates. *Journal of Human Evolution* 22: 469–493.
- Dunbar, R. 1993. Coevolution of Neocortical Size, Group Size and Language in Humans. *Behavioral and Brain Sciences* 16: 681–694.
- Eller, E., J. Hawks, and J. H. Relethford. 2004. Local Extinction and Recolonization, Species Effective Population Size, and Modern Human Origins. *Human Biology* 76: 689–709.
- Frank, S. A. 1995. George Price’s Contributions to Evolutionary Genetics. *Journal of Theoretical Biology* 175: 373–388.
- Guglielmino, C. R., C. Viganotti, B. Hewlett, and L. L. Cavalli-Sforza. 1995. Cultural Variation in Africa: Role of Mechanisms of Transmission and Adaptation. *National Academy of Sciences, Proceedings* 92: 7585–7589.
- Haberle, S. G., and B. David. 2004. Climates of Change: Human Dimensions of Holocene Environmental Change in Low Latitudes of the PEPHII Transect. *Quaternary International* 118–119: 165–179.
- Harpending, H. C., S. T. Sherry, A. Rogers, and M. Stoneking. 1993. The Genetic Structure of Ancient Human Populations. *Current Anthropology* 34: 483–496.
- Henrich, J. 2004. Demography and Cultural Evolution: How Adaptive Cultural Processes Can Produce Maladaptive Losses—The Tasmanian Case. *American Antiquity* 69: 197–214.
- Henrich, J., and R. Boyd. 2002. On Modeling Cognition and Culture: Why Cultural Evolution Does Not Require Replication of Representations. *Journal of Cognition and Culture* 2(2): 87–122.
- Henrich, J., and F. J. Gil-White. 2001. The Evolution of Prestige: Freely Conferred Deference as a Mechanism for Enhancing the Benefits of Cultural Transmission. *Evolution and Human Behavior* 22: 165–196.
- Henshilwood, C., F. d’Errico, M. Vanhaeren, K. van Niekerk, and Z. Jacobs. 2004. Middle Stone Age Shell Beads from South Africa. *Science* 304: 404.
- Hudjashov, G., et al. 2007. Revealing the Prehistoric Settlement of Australia by Y Chromosome and mtDNA Analysis. *National Academy of Sciences, Proceedings* 104: 8726–8730.
- James, H. V. A., and M. D. Petraglia. 2005. Modern Human Origins and the Evolution of Behavior in the Later Pleistocene Record of South Asia. *Current Anthropology* 46: S3–S27.
- Klein, R. G. 2000. Archaeology and the Evolution of Human Behavior. *Evolutionary Anthropology* 9: 17–36.
- Lahr, M. M., and R. A. Foley. 1998. Towards a Theory of Modern Human Origins: Geography, Demography, and Diversity in Recent Human Evolution. *Yearbook of Physical Anthropology* 41: 137–176.

- Lahr, M. M., and R. A. Foley. 2003. Demography, Dispersal and Human Evolution in the Last Glacial Period. In *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, edited by T. H. van Andel and W. Davies, pp. 241–256. McDonald Institute for Archaeological Research, Cambridge.
- Lombard, M. 2008. Finding Resolution for the Howiesons Poort through the Microscope: Micro-residue Analysis of Segments from Sibudu Cave, South Africa. *Journal of Archaeological Science* 35: 26–41.
- Lumsden, C. J., and E. O. Wilson. 1981. *Genes, Minds and Culture*. Harvard University Press, Cambridge, Mass.
- Marean, C. W., et al. 2007. Early Human Use of Marine Resources and Pigment in South Africa during the Middle Pleistocene. *Nature* 449: 905–908.
- McBrearty, S., and A. S. Brooks. 2000. The Revolution That Wasn't: A New Interpretation of the Origin of Modern Human Behavior. *Journal of Human Evolution* 39: 453–563.
- Mellars, P. 2005. The Impossible Coincidence: A Single-Species Model for the Origins of Modern Human Behavior in Europe. *Evolutionary Anthropology* 14: 12–27.
- O'Connell, J. F., and J. Allen. 2004. Dating the Colonization of Sahul (Pleistocene Australia–New Guinea): A Review of Recent Research. *Journal of Archaeological Science* 31: 835–853.
- O'Connell, J. F., and J. Allen. 2007. Pre-LGM Sahul (Pleistocene Australia–New Guinea) and the Archaeology of Early Modern Humans. In *Rethinking the Human Revolution*, edited by P. Mellars, K. Boyle, O. Bar-Yosef, and C. Stringer, pp. 395–410. McDonald Institute for Archaeological Research, Cambridge.
- Peck, J. R. 1996. Limited Dispersal, Deleterious Mutations and the Evolution of Sex. *Genetics* 142: 1053–1060.
- Peck, J. R., G. Barreau, and S. C. Heath. 1997. Imperfect Genes, Fisherian Mutation and the Evolution of Sex. *Genetics* 145: 1171–1199.
- Price, G. R. 1970. Selection and Covariance. *Nature* 227: 520–521.
- Rogers, A. R. 1995. Genetic Evidence for a Pleistocene Population Explosion. *Evolution* 49: 608–615.
- Shennan, S. J. 2000. Population, Culture History, and the Dynamics of Culture Change. *Current Anthropology* 41: 811–835.
- Shennan, S. J. 2001. Demography and Cultural Innovation: A Model and Its Implications for the Emergence of Modern Human Culture. *Cambridge Archaeological Journal* 11: 5–16.
- Shennan, S. J., and J. Steele. 1999. Cultural Learning in Hominids: A Behavioral Ecological Approach. In *Mammalian Social Learning: Comparative and Ecological Perspectives*, edited by H. Box and K. Gibson, pp. 367–388. Cambridge University Press, Cambridge.
- Sherry, S. T., A. R. Rogers, H. Harpending, H. Soodyall, T. Jenkins, and M. Stoneking. 1994. Mismatch Distributions of mtDNA Reveal Recent Human Population Expansions. *Human Biology* 66: 761–775.
- Stiner, M. C., and S. L. Kuhn. 2006. Changes in the “Connectedness” and Resilience of Paleolithic Societies in Mediterranean Ecosystems. *Human Ecology* 34: 693–712.
- Tindale, N. B. 1953. Tribal and Intertribal Marriage among the Australian Aborigines. *Human Biology* 25: 169–190.
- van Andel, T. H., W. Davies, B. Weinger, and O. Jöris. 2003. Archaeological Dates as Proxies for the Spatial and Temporal Human Presence in Europe: A Discourse on the Method. In *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, edited by T. H. van Andel and W. Davies, pp. 21–29. McDonald Institute for Archaeological Research, University of Cambridge, Cambridge.
- Vanhaeren, M. 2005. Speaking with Beads: The Evolutionary Significance of Personal Ornaments. In *From Tools to Symbols from Early Hominids to Humans*, edited by F. d'Errico and L. Blackwell, pp. 525–553. Wits University Press, Johannesburg.
- White, T. D., B. Asfaw, D. DeGusta, H. Gilbert, G. D. Richards, G. Suwa, and F. C. Howell. 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423: 742–747.
- Zilhão, J. 2007. The Emergence of Ornaments and Art: An Archaeological Perspective on the Origins of “Behavioral Modernity.” *Journal of Archaeological Research* 15: 1–54.