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Beyond the Tools: Social Innovation and Hominin Evolution

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ABSTRACT

Archaeological interest in innovation traditionally focuses on creativity in material culture and, in the case of the Paleolithic, particularly on the changing morphology of stone tools. However, this is only one result of a constellation of innovative processes that occur both between and within hominin groups evolving towards the unique modern human lifeway. The adaptations scaffolding such innovative processes include not only the cognitive mechanisms and biological and skeletal adaptations that underpin technological innovation and cultural transmission, but also the behavioral strategies pursued by hominin groups and individuals. In this paper, we draw from a Social Brain approach to argue that it is hominins' innovative social and group-oriented behavioral strategies that drive technological developments and distinguish us from other primates. A variety of models and methodologies developed to investigate the interrelationships between the crucial ecological, social, and behavioral variables are reviewed here for an archaeological audience in order to stimulate research to test and refine these models with archaeological data.

The "Innovation and Evolution" workshop was held at the Centre for the Archaeology of Human Origins, University of Southampton, United Kingdom; workshop papers guest edited by Hannah Fluck (University of Southampton; and, Landscape, Planning and Heritage, Hampshire County Council), Katharine MacDonald (Faculty of Archaeology, University of Leiden), and Natalie Uomini (School of Archaeology, Classics and Egyptology, University of Liverpool). This is article #2 of 7.

INTRODUCTION

In this paper we wish to broaden the focus of the archaeological investigation of innovation and to place it in a broader evolutionary context than one focusing purely on the changing material forms of stone tools. Figure 1 identifies some of the major factors involved in hominin evolution, and it is immediately clear that the human niche is the product of a complex balance of factors. Different variables are likely to have been stressed at different times and in different contexts, and some of these are more tightly coupled than others. Nevertheless, it is clear that any simple, linear 'prime mover' explanation for hominin evolution would be naïve (e.g., Foley 1995: 69). Further, while some of these variables clearly relate to biological evolution and/or ecological adaptations, other factors are more usually thought of as 'social' or 'cultural.' As Figure 1 makes clear, however, this is in many ways a false dichotomy; there is less a division than a continuum between the biological and the cultural.

Crucial to the debate are our definitions of innovation and intelligence; as we shall see, these are necessarily bound together with notions of creativity and flexibility. While the term 'innovation' is ambiguous in that it can refer to both the product and the process, *an* innovation is simply something new (Adams et al. 2006). Note, however, that the Latin verb *innovare* from which the English *innovation* derives suggests renewal; thus innovation can be seen as akin to an evolutionary rather than a revolutionary process, with each new aspect being a modification of a previous model (Baregheh et al. 2009). Whether a given innovation is incremental or radical then depends on the magnitude of the effects of the modification (Kahn et al. 2003)—as, indeed, in biological evolution, where certain evolutionary changes are viewed as 'major transitions' only with hindsight (Szathmary and Smith 1995).

It is also of considerable importance to distinguish between innovation and transmission—innovations can be viewed as a subset of the variation available to selection (whether genetic or cultural). Only successful (note, not always the most 'useful') innovations will be transmitted to a large sector of the population, and thus such innovations either are (in the biological case) or are directly analogous to (in the cultural case) traits with high relative fitness. From an archaeological perspective, it is vital to note that

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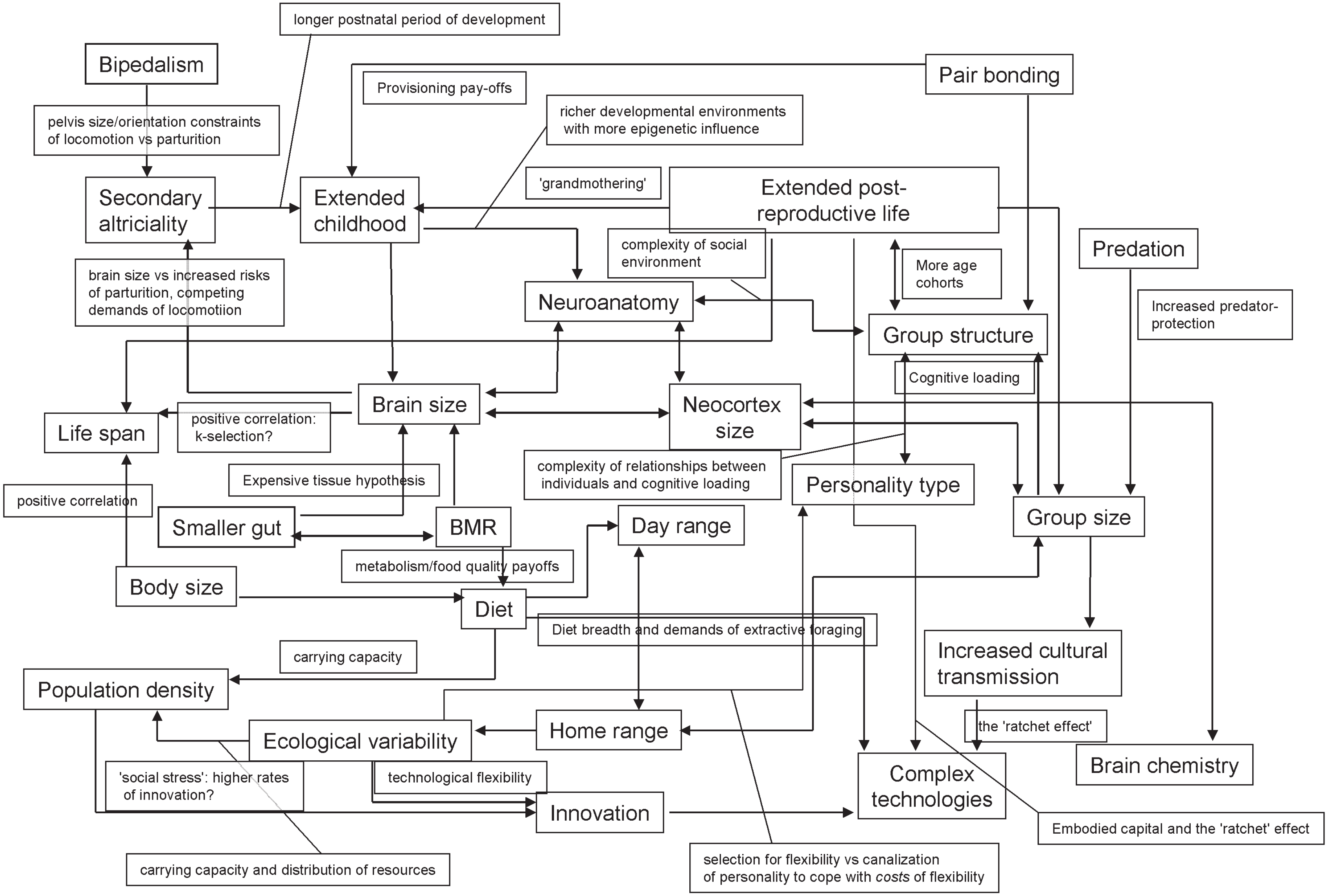

Figure 1. Some variables in hominin evolution.

unsuccessful innovations will rarely be visible to us and that, when they are, their paucity may make them difficult to interpret, for example, in the case of early putative 'symbolic artifacts' (e.g., Chase and Dibble 1992; d'Errico and Nowell 2000; Noble and Davidson 1996). In what follows, we therefore adopt the simple definition of an innovation as something new to hominin lifeways, whether an artifact, a behaviour, or a form of social organization. A creative individual is one who has a propensity to innovate, and thus we follow Lefebvre and colleagues (Lefebvre et al. 1997, 1998, 2002; Reader and Laland 2001, 2002, 2003; Sol et al. 2002; Sol, Duncan et al. 2005; Sol, Lefebvre et al. 2005, 2007) in operationally equating creativity with 'innovativeness.' Below, we consider how creativity relates to intelligence and the extent to which both facilitate behavioral flexibility.

INNOVATION, INTELLIGENCE AND ENCEPHALIZATION

Macro-scale relationships between environment, cognition, and innovativeness are fundamental to what can perhaps be termed the 'standard model' of hominization. However, as Figure 1 clearly demonstrates, their interrelationships are more complex than is often recognised by approaches equating (if only implicitly) encephalization with intelligence, and intelligence with behavioral flexibility. Among many non-human species for which data exist, behavioral flexibility and innovativeness do correlate well with various measures of brain size. Among birds, brain size corrected for body weight (Sol et al. 2002), forebrain size (Lefebvre et al. 1997, 1998; Nikolakakis and Lefebvre 2000), and the relative size of the hyperstriatum-neostriatum complex (Lefebvre et al. 2004; Reader 2003; Timmermans et al. 2000) are all good predictors of behavioral flexibility, rates of neophilia, or the propensity to innovate. Among primates alone, cross-species frequencies of innovation also correlate with measures of both relative and absolute executive brain volume. Social learning and tool use also correlate with executive brain size (Reader and Laland 2001, 2002).

Among modern humans, however, the lack of any correlation between various measures of brain size and IQ (e.g., Jensen and Sinha 1993; Rushton and Ankney 1996; van Valen 1974; Wickett et al. 1994; Witelson et al 2006) or number of cortical neurons (Haug 1987: 135; Witelson et al 2006), as well as the ambiguous relationship between IQ and creativity itself (Barron and Harrington 1981; Heilman et al. 2003; Herr et al. 1965; Simonton 1999; Torrance 1975), sound a cautionary note against assuming straightforward relationships between simple brain metrics and complex aspects of cognition. While the above-mentioned studies report intra-species relationships and cannot be reliably extrapolated to evolutionary reconstructions comparing different species, they do cast doubt on the simplistic assumption that a larger brain is inherently better at all tasks encountered by the animal. In particular, and as Falk and colleagues (2009) have recently made clear, aspects of brain reorganization may have been at least as important as generic encephalization in the course of hominin evolution. As a result, although the trajectory of hominin brain size evolution over the past 3 million years is now reasonably well known (see also Ash and Gallup 2007; De Miguel and Henneber 2001; Falk 2007; Holloway et al. 2004; Lee and Wolpoff 2003), extrapolation from these data to infer cognitive abilities should be practiced with caution (see also Falk et al. in press).

Traditionally, psychologists have focused on the mechanisms through which novelty in innovative or creative behavior arises, emphasizing novel associations between previously distinct ideas or areas of thought (James 1890: 457; Poincaré 1913: 386; Spearman 1927; see also Kyriacou and Bruner this volume.). In this vein, Mednick (1962: 221) developed a working definition of 'creativity' in terms of the 'remoteness' of the elements it combined, allowing him to quantify 'novelty' in a word association task by measuring the novelty of combinations of individual words (see also Bousfield et al. 1954). The neurological correlates of innovativeness thus defined also are beginning to be identified; it has long been known that neuromodulators associated with stress can suppress the likelihood of remote associations (Easterbrook 1959; Mintz 1969) by impacting negatively on the spread of activation in semantic networks in the brain (Beversdorf et al. 1999; Heilman et al. 2003; Kischka et al. 1996), and it now appears that the opposite conditions might apply in conditions such as schizophrenia and autism. Recent research into these conditions has suggested they might represent a low signal-to-noise ratio (*sensu* Cohen and Servan-Schreiber 1992, 1993; see also Snyder 2009), making it difficult for subjects to integrate inputs coherently (Frith and Happé 1994: 121; see also Frith 1989), possibly resulting from a failure in inhibitory top-down processing constraints (Snyder 2009). The broad (though largely anecdotal) literature that exists on instances of creativity and remarkable specific cognitive feats among schizotypic and autistic individuals, respectively, is certainly suggestive of a link with innovativeness (e.g., Brune 2004a, 2004b; Bolte and Poustka 2004; Burch et al. 2006; Kelly et al. 1997; Miller and Tal 2007; Nettle 2001; Nettle and Clegg 2006; Pring and Hermelin 2002; though see also Keller and Miller 2006; see also Jamison 1993 for discussion of the links between creativity and bipolar disorder).

At the neurological level, then, it would seem that cognitive flexibility is related not to brain size or number of neurons, but on their connectivity (e.g., Cajal 1989: 459) and on the context of neurological activity—which are strongly dependent on a variety of 'social' factors (Grove and Coward 2008; Coward and Grove submitted). It has long been recognized that adaptation occurs in response to the social as well as the physical environment (e.g., Reader and Laland 2001: 148; see also Reader and Laland 2003 for further definitions), but this has often been overlooked in accounts of human evolution, and in this paper we draw from a Social Brain (Dunbar 2003) approach as a corrective to traditional technologically-obsessed accounts of hominin evolution, focusing instead on some of the biological, ecological, and social innovations that characterize the hominin niche.

We begin below with the macro-scale 'standard model' of hominization, focusing on climatic and environmental factors as drivers of hominin innovation as evidenced through evolving material culture, and subsequently focus in on successively finer scales to investigate the innovative social and group-oriented behavioral strategies developed in the hominin lineage at a population level, then at local network level and finally at the intra-group and individual levels of variation. It is the adaptations to variability and flexibility at these much more intimate scales, we argue, that really make humans distinctive.

THE 'STANDARD MODEL' OF HOMININ EVOLUTION: INNOVATION, ENVIRONMENT, AND CLIMATE

The extent to which specific behaviors are learned and passed down between generations often has been considered a defining characteristic of humans. However, more recent research has demonstrated that often significant parts of the behavioral repertoires of many other animal species are neither determined by genetics nor individually acquired via trial-and-error but learned from conspecifics (Brown and Laland 2003; Ford 1991; Fritz and Kotraschal 1999; Franks and Richardson 2006; Krützen et al. 2005; Poole et al. 2005; papers in Box and Gibson 1999; Eerkens and Lipo 2007 for review). This is especially true among hominoids (Breuer et al. 2005; McGrew 1992; van Schaik 1996), where many consider the behaviors concerned both group-specific and sufficiently persistent through time to merit their description as 'cultures' (e.g., van Schaik et al. 2003; Whiten 2005; Whiten and Boesch 2001; Whiten and van Schaik 2007; Whiten et al. 1999); interestingly, some of these behaviors include tool-related behaviors that may leave material traces (e.g., McGrew 1992; Mercader et al. 2002, 2007; Haslam et al. 2009). Nevertheless, among humans the diversity and complexity of behaviors learned from others by far outstrips anything known in other species. Crucially, human cultural transmission is also *cumulative* in a way that other species' socially learned repertoires are not (Boyd and Richerson 1996; Tomasello 1999; Tomasello et al. 1993).

What determines the balance between individual innovation and social learning? The basic rationale for the adaptiveness of cultural transmission is that it allows individuals to save themselves the costs of learning. However, this is only the case in certain situations. The mathematical models of Boyd and Richerson (1985, 1996, 2005) suggest that 'rates of both innovation and innovation adoption will be variable and respond to variation in social, economic, and environmental conditions' (2005: 335). For example, frequency-dependent biased cultural transmission is a highly efficient strategy in relatively stable environmental and social circumstances, saving the cost of evaluating different options as well as the potential risks of trial-and-error learning and innovation. They suggest that cultural transmission is likely to be favored over genetic transmission and individual learning only where significant but relatively predictable environmental fluctuations occur, conditions in which innovations resulting from individual trial-and-error learning would make only relatively slight improvements to individuals' phenotypes but cumulative cultural change would allow the development of specific fitness-enhancing adaptations to particular environments on time scales of decades or millennia (Boyd and Richerson 2005; Richerson et al. 2005, 225; see also Boyd and Richerson 1996; Henrich and McElreath 2003; Tomasello 2000; Tomasello et al. 1993).

In contrast, according to Potts' variability selection hypothesis (VSH) behavioral and cognitive flexibility are likely to be adaptive under conditions of environmental variability (Potts 1998b: 112). Temporal variation in the climatic regime and its associated selective environment have become significantly more prominent during the last five million years (deMenocal 1995, 2004; deMenocal and Bloemendal 1996; Muller and MacDonald 1997), suggesting that mechanisms for individual learning should have been favored over cultural transmission among some species—including hominins (Potts 1998b: 85). In support of the view that environmental change promotes behavioral flexibility, Sol and colleagues (2002, 2005a, 2005b) found fewer instances of innovative behavior in migratory than sedentary bird species; furthermore, the latter were found to exhibit greater frequencies of innovative behaviors during winter months when staple summer foods were largely unavailable (Sol, Lefebvre et al. 2005). Perhaps unsurprisingly, bird species with larger brains and higher frequencies of foraging innovations (many relating to tool use; Lefebvre et al 2002; Reader 2003; Reader and Laland 2002) were more successful on introduction to novel environments than less innovative, smaller-brained species (Duncan et al. 2003; ; Sol, Duncan et al. 2005; Sol and Lefebvre 2000; Sol et al. 2002). This would suggest that innovativeness and migration may be alternative responses to seasonal and longer-term environmental variability respectively, and relate to different biological evolutionary strategies.

In fact, there are strong positive correlations between measures of both social learning and innovation *and* brain size across a wide variety of species (Bouchard et al 2007; Reader 2003; Reader and Laland 2002), suggesting that the two might ultimately draw on the same underlying cognitive processes, not polar opposites but complementary behavioral strategies which may be variably stressed in different environmental contexts. It is likely that, in order for innovativeness to be adaptive, it must be coupled with adequate social transmission of the novel behavior among conspecifics; together, these may lead to accelerated rates of evolution and higher speciation rates (Nikolakakis et al. 2003; see also Wilson 1985 for discussion of the 'behavioral drive hypothesis'). This observation implicates demographic factors in the evolution of both social learning and innovation.

INNOVATION, FORAGING, SUBSISTENCE, AND TECHNICAL INTELLIGENCE

Environmental factors may also have much more specific effects on animals' behavior through their impact on the ecological distribution of particular resources. In particular, more energetically rewarding foodstuffs (such as ripe fruits) are more patchily distributed both temporally and geographically than lesser-quality resources (such as leaves or grass). This has a significant impact on the sizes of home ranges observed in species pursuing different foodstuffs; frugivorous primates are forced to cover larger geographical areas to meet their energy requirements than species specializing on young leaves or mature foliage.

These different dietary and foraging strategies may select for more variable 'mental mapping' abilities; among primates specializing on fruit, for example, cognitive mechanisms for remembering or 'mapping' sources within their range in four dimensions should be adaptive—although the temporal schedules of fruit items are restricted, they are nevertheless highly predictable, often over many years. In addition, while resources such as leaves are predictable in the mid-term, they are unlikely to persist unchanged over inter-generational timescales, favoring social learning over genetic mechanisms for vertical dissemination of this form of knowledge (Milton 1981). Frugivorous spider monkeys, for example, have considerably larger home ranges and brain weights approximately double those of similar-sized (leaf-eating) howler monkeys (Milton 1988; though see Reader and MacDonald 2003). However, the experimental evidence for more sophisticated mental mapping skills among frugivorous primates is mixed (Janson and Byrne 2007; Reader and MacDonald 2003). Among howler monkeys, more cohesive groups also may provide a continuous stream of foraging information, reducing the pressure on individuals to acquire new knowledge (Milton 1981; see also Cunningham and Janson 2007; di Fiore and Suarez 2007; Janson 2007; Normand and Boesch 2009; Noser and Byrne 2007; Valero and Byrne 2007).

Of course, investigation of the potential correlations between brain size and dietary strategies is somewhat complicated by the strong positive correlation between brain size and basal metabolic rate (BMR; Martin 1981, 1982), which means that the metabolically expensive brain can only become larger among species 'who can sustain high caloric intake relative to energy expenditure on a year-round basis' (Gibson 1986: 93). One means of doing this is through biological evolutionary trade-offs such as reducing the size of the gut, thus freeing up capacity in the energy budget for encephalization (Aiello 1998; Aiello and Wheeler 1995). However, energetic costs can also be offset by innovative behavioral strategies which allow the specialized procurement of particular foods and/or the pre-ingestion processing of food items. For example, mountain gorillas have learned to eat nettle leaves by rolling them into bundles with the stinging surface of the leaf in the center, away from sensitive mouth parts (Byrne and Byrne 1993). Human cooking is another such example (Wrangham et al. 1999)

Other innovative behavioral strategies involve extractive foraging—'feeding on foods that must first be removed from other matrices in which they are embedded or encased' (Gibson 1986: 97); e.g., the separation of flesh from bones or shells before ingestion. These strategies are predictably highly correlated with tool use (Gibson 1986: 536–545; see also Reader and Laland 2003; also Goodall 1986, Whiten et al. 1999 for examples from chimpanzee tool use). By increasing foraging efficiency, such technological innovations can have potentially powerful effects on time budgets and thus on social strategies (compare, e.g., Byrne 1995; Dunbar 2003; Dunbar et al. 2009; Zuberbühler and Byrne 2006). Recent modelling work has begun to demonstrate how ecological constraints shape group size and structure directly via resource availability and indirectly via reduced time for the social bonding necessary for longer-term group cohesion (e.g., Dunbar 1992c, 1996; Korstjens et al. 2006; Korstjens and Dunbar 2007). The fission-fusion social system characteristic of chimpanzees (and various other mammals including humans) may be one mechanism for dealing with ecological constraints (Lehmann et al. 2007).

The obvious cognitive demands of tool manufacture, selection, and use also are likely to be of importance. Significantly, apes appear to have a much greater understanding of the technical properties of materials and the relations between them than monkeys (Byrne 1995). All great apes use tools both in the wild and in captivity (e.g., Breuer et al. 2005; Goodall 1986; van Schaik 1996), demonstrating a sophisticated understanding of the temporal structure of tool-using tasks, for example, using a 'tool-set' in which each tool has a specific function in achieving the final goal while termite-fishing at Ndoki (Suzuki et al. 1995). Among monkeys, only capuchins (who have a very high neocortex ratio) have demonstrated any skill with tools (Canale et al. 2009; Mannu and Ottoni 2009; Ottoni and Izar 2008). However, while early experiments suggested that capuchins' tool use, in contrast to that of chimpanzees, for example, demonstrated little or no understanding of cause and effect (Visalberghi and Fragaszy 1990; Visalberghi and Limongelli 1994; Visalberghi and Trinca 1989), more recent observations on wild populations have since suggested their abilities in this area may have been underestimated and that they are able to select appropriate tools and plan actions (Mannu and Ottoni 2009; Visalberghi 2009), suggesting that the cognitive mechanisms involved have a long evolutionary history and that the contexts of their expression are highly significant.

The major components of what we refer to as the 'standard model' of hominin evolution thus reference large-scale climatic and environmental patterning as the primary selective environment for the evolution of the cognitive mechanisms underlying behavioral flexibility and innovation. Clearly, these factors do play an extremely important role in the process of hominization. Nevertheless, it would seem that they are only part of the overall constellation of selective pressures and constraints, adaptations, exaptations, and behavioral strategies that resulted in modern human lifeways. Innovativeness is itself an innovative strategy, clearly underpinned by a number of significant biological adaptations which positioned hominins advantageously at a peak in the fitness landscape defined by significant behavioral flexibility. However, the underlying cognitive capacities for learning and imitating are fundamentally social, and these biological, cognitive, technological, and behavioral adaptations to the physical environment cannot be separated out from the highly social environments in which they occurred and which will be examined at successively finer scales in the rest of this paper.

THE SOCIAL MODEL OF HOMININ EVOLUTION: INNOVATION AND LIFE HISTORY

Many species other than humans engage in cultural transmission via social learning, and the basic capacity for imitation—the mirror neuron system, which automatically maps the observed actions of others onto one's own motor system—is part of our primate heritage (Gallese et al. 2004). However, while other species may *learn* behaviors, and even act in such a way as to facilitate their offspring's learning (known as 'social enhancement'), only humans are known to *teach*, actively correcting learners (Tomasello 1999). One potential basis for this difference that has been suggested recently is that the hominin mirror neuron system may be the basis for a theory of mind (ToM) which allows us to go beyond simply imitating the observed motor acts of others to infer their intentions and perhaps even their states of mind (Gallese 2006)—perhaps the prerequisite for true imitation, teaching, and cumulative cultural transmission (Knoblich and Sebanz 2008; Tomasello et al. 2005; though see, e.g., Borg 2007; Saxe 2009).

However, neither humans nor primates are born fully-fledged imitators or mind-readers. The necessary cognitive and motor systems take time to mature, and the importance of external as well as genetic factors during development suggests that ontogenetic as well as phylogenetic influences are a significant factor. While primates as a whole are a precocial order, with young born relatively developed after a long gestation, they display delayed motor development which in modern humans is so extreme that we have been dubbed 'secondarily altricial.' It takes a human newborn a full year to reach the stage of motor development equivalent to that of a newborn great ape (Smith and Tompkins 1995). Most brain growth in human newborns occurs after birth—while the brains of apes in general are 40% of adult size at birth, the figure for human neonates is only ~29% (see Coward and Grove submitted; DeSilva and Lesnik 2006; though see also Leigh 2004 for discussion of the significance of variable rate versus duration of hominoid brain development). The neural architecture of the brain is genetically underspecified and reliant instead on the relatively indiscriminate proliferation of new connections during early development—connections which are subsequently pruned by axonal competition for limited synaptic targets and programmed cell death for those that fail (Coqueugniot et al. 2004; Deacon 1997; Donald 1991). Among humans, most of this process takes place while the individual is already interacting with the social environment, massively extending the degree to which the selective effects of experience can impact on the developing synaptic connections (see Coward and Grove submitted; Grove and Coward 2008 for further discussion). This expanded period of development and maturation of the brain in increasingly rich social and cultural environments is likely to have facilitated the cumulative cultural transmission of behavior, suggesting that these innovations in life history among hominins may have been at least partly selected for by the adaptiveness of cumulative cultural transmission (itself an innovative behavior; Boyd and Richerson 1996). While studies disagree over the relative importance of cultural transmission of subsistence or social skills (see, e.g., Barrickman et al. 2007; Gurven et al. 2006; Joffe 1997; MacDonald 2007 for discussion), it is clear that many complex cultural skills of modern humans take substantial periods of intensive teaching and/or practice and observation to master—several years in some cases (Hosfield 2009; see also MacDonald 2007; Shennan and Steele 1999; Stout 2002).

Drawing from the notion of capital in economics, one argument linking the large brains, altricial offspring, extended juvenile periods, long lifespans, and multi-generational societies of hominins posits the selective advantage of 'embodied capital' (Kaplan et al. 2000, 2003a, 2003b). This may be conceived of in a physical sense, as 'organized somatic tissue' such as muscle and brain, or in the broader sense of 'strength, skill, knowledge, and other abilities' (Kaplan and Robson 2002: 10221). Extended juvenile periods of modern humans represent increased investment in a resource—brain tissue and the abilities it enables—that will yield returns only later in life. The human strategy represents a balancing act between early investment and later returns that is strongly affected not only by the biological but also by the eco-social context of selection (see, e.g., Coward and Grove submitted for further discussion).

The fossil record documents a gradual shift in life histories during hominization, and in particular an extension of the period of postnatal dependency (Coward and Grove submitted; Coqueugniot et al. 2004; DeSilva and Lesnik 2008; Robson and Wood 2008; Smith and Tompkins 1995). Stone tools appear in the archaeological record from at least 2.5 mya (Semaw et al. 1997), and their use is attested to from 3.3 mya (McPherron et al. 2010), providing evidence of sufficient social and technical skills for the habitual appropriation of more energetically efficient foodstuffs, notably bone marrow and meat among at least some australopithecines and certainly among early *Homo*. This dietary shift in turn made it easier to provision the longer developmental timetable, which required the involvement of more than one adult—an indication of more complex and longer-lasting social relationships. This may have been achieved through communal or co-operative breeding strategies (Isler and van Schaik 2009: 394; Mace and Sear 2005) including parental pair-bonding (which also may have selected for cognitive abilities; Dunbar and Shultz 1997) and/or 'grandmothering' (see, e.g., Peccei 2001 for review; also Caspari and Lee 2004; Hawkes et al. 1998; Peccei 1995). Significantly, longer post-reproductive survival (Caspari and Lee 2004) also is likely to have had important ramifications for the vertical transmission of embodied capital in the form of elders' acquired knowledge.

INNOVATION AND DEMOGRAPHY

These developments in life-history strategies will of course also have had important ramifications for hominin demography. Demographic factors such as population density have a significant effect on both the occurrence of novel social contexts requiring innovative behaviors *and* the rate and scale of the diffusion of the resultant innovations, thus structuring both their appearance and their distribution in the archaeological record. However, the relationships between demography, innovation, and diffusion are by no means straightforward. Of course, if a constant per capita innovation rate is assumed, larger populations are obviously more likely to generate innovation than smaller populations, and simulation studies provide some evidence for the intuitive idea that large populations have an advantage in the generation and dissemination of innovations (Shennan 2001: 12; see also Powell et al. 2009). However, other models posit almost exactly the opposite, suggesting that social learning (in the sense of imitation of others) may be more adaptive than innovation (as the product of trial-and-error learning) in strong social contexts such as large groups. Early technologies demonstrate a notoriously limited variability in both time and space—nevertheless, they do display a high level of technological skill and investment, leading Mithen (1996) to infer strong cultural traditions and social learning skills among early Paleolithic hominin groups. He argued that much of the variability among assemblages might be directly attributable to variability in the demographic and social factors influencing artifact manufacture (Mithen 1996: 216). Mithen's central argument is that in small groups artifacts are likely to be more diverse due to the weak influence of cultural traditions and the limited skills acquired with no effect of cumulative technical experience, whereas greater competition in larger groups might lead to the emergence of social norms of artifact production mediated by increased levels of social learning (Mithen 1996).

Given the strong links between group size and environment already discussed, group size is also likely to be strongly related to environmental factors. Thus Mithen goes on to associate glacial/open environments with large group size (because of predation pressure; see Figure 1) and strong cultural traditions and inter-glacial wooded landscapes with small group size and weak cultural traditions (although the correlations Mithen drew between open and wooded environments and handaxe/non-handaxe traditions has been heavily criticized; e.g., McNabb and Ashton 1995). In addition, the linking or separation of discrete groups through expansion and contraction of contact ranges is also an important factor, with larger *effective* population sizes having significant effects on the complexity of cultures that can be maintained (e.g., Kline and Boyd 2010; Shennan 2001). Changing environmental conditions and/or subsistence strategies impacting on contact between groups and thus effective population size can thus have a potentially very significant effect on material culture and the archaeological record, as documented by Henrich (2004) for Holocene Tasmania, where rising Holocene sea-levels cut the island off from the wider social networks of the Australian mainland and led to a drastic reduction in effective population size and the loss of a number of complex skills—including, as perhaps might have been predicted by Mednick's (1962) findings, discussed above, composite technologies.

It is this strong interrelationship between demography and the transmission of cultural traits that led Cullen to draw an analogy with viruses (1996: 426). Like viruses, cultural innovations need very particular social conditions to spread—most notably, as mentioned above, large connected populations who can 'infect' one another. Knight et al. (1995) have suggested that the so-called Upper Paleolithic 'revolution' may have had less to do with restricted cognitive ability on the part of Neanderthals and more to do with demographics and distributions of Upper Paleolithic populations. As Cullen writes,

> 'we may suggest that the habitat or niche to which cultural phenomena are adapted (communities of hominids with a fully developed cultural capacity) was unevenly distributed and highly unreliable throughout most of the Lower and Middle Palaeolithic. When new ideas appeared in one community there may have been very few opportunities for that idea to have been taught to individuals of other communities some distance away ... The long-term survival of the distinctive cultural phenomena which characterize Upper Palaeolithic and later assemblages would, I propose, have required the existence of extensive coalitions between people distributed over a wide area, and maintained through a continuous fabric of social interaction' (1996: 425).

Indeed, the analogy has been pursued through the use of epidemiological models of the adoption and dissemination of innovations in very similar ways to those used to investigate the transmission of disease (Boyd and Richerson 1985; Dodds and Watts 2005). By and large these are essentially modifications of an epidemiological model first developed by Hamer (1906, cited in McGlade and McGlade 1989), and assume homogeneous populations in whom 'infection' (or the spread of a specific trait) is governed only by the infectiousness/adaptiveness/attractiveness of the trait and/or by initial outbreak size (see Figure 2 for example of typical output from an SIR model). Models also often assume no interdependency between contacts; the probability of 'infection' is usually assumed to be independent and identical at each contact. As we will discuss below, these assumptions are inappropriate for modelling social 'contagion' (and, indeed, are oversimplified even for modelling biological infection in many cases [e.g., Buchanan 2002: Chapter 11; Lindenbaum 1978]). Human populations are neither homogeneous nor evenly distributed in space or time.

INNOVATION IN SOCIAL NETWORKS

One significance advance on these highly simplified models has been to allow 'dose sizes' and 'thresholds' to vary (e.g., Dodds and Watts 2005)—in short, to make the *social relationship* between the individuals and the *context* of their

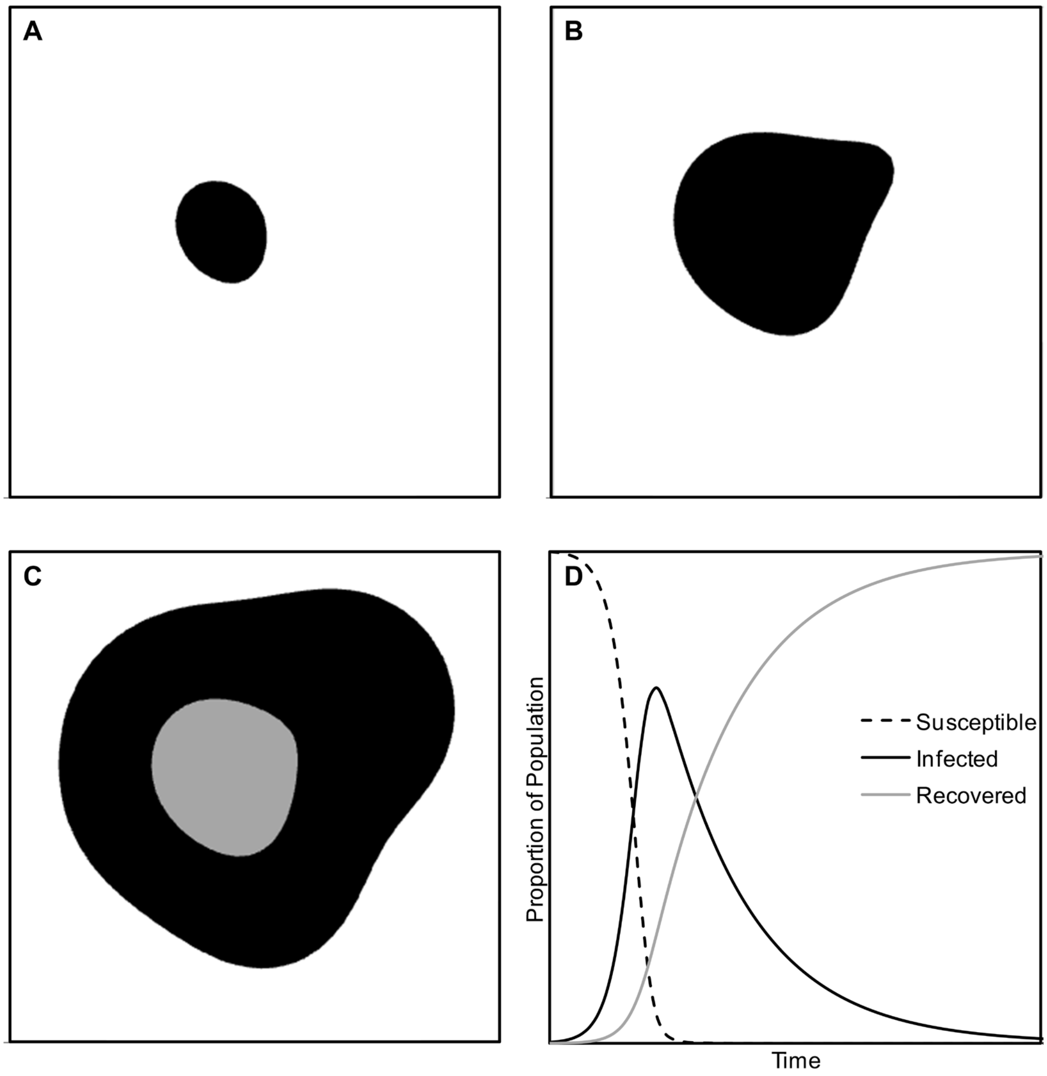

Figure 2. A-C, snapshots of a spatial SIR model. Susceptible, infected, and recovered individuals are represented by white, black and grey shaded areas respectively. D plots the dynamics of susceptible, infected, and recovered individuals over time for a typical model run. The sigmoid decline of susceptible individuals mirrors the pattern of spatial innovation diffusion proposed by Hagerstrand (1967) and others.

encounter a significant factor in the process. For example, the adoption of a particular behavior practised by someone else—such as the purchase of a particular brand of handbag sported by a favorite celebrity—will be affected by a variety of factors including the individual's susceptibility to new stimuli (whether or not they believe said celebrity to be an appropriate role model), their exposure to the behavior (whether or not they read Heat magazine), their immediate ability to adopt the behavior (whether they have the economic wherewithal), and so on. Boyd and Richerson's notion of 'bias' (1985; 2005) is one way of addressing at least some of these factors but perhaps does not go far enough.

In addition, some models of diffusion recognize that populations are not homogeneous, distinguishing between sub-groups in terms of the timing of their adoption of innovations: 'innovators,' 'early majority,' 'late majority,' and 'laggards' (McGlade and McGlade 1989: Figure 14.1). However, even this is oversimplified: Hägerstrand's Monte Carlo simulations (1952, 1967) demonstrated that while the phased acceptance of innovation is best described by equations producing travelling waves, these are highly affected by contextual factors such as the regularity and quality of interpersonal contact and communication. Furthermore, adopter categories are unlikely to reflect the complexity of processes of adoption/rejection of particular innovations and their timing, which are situation-specific and highly contextual (McGlade and McGlade 1989: 285–7). In short, it is simply not possible to consider issues of innovation and creativity, social learning and cultural transmission without tackling the individual relationships that lie at the heart of these processes; while much of this work was done some time ago, these findings have not been followed up to any significant extent, and a natural progression, as recently suggested by Dodds and Watts (2005: 599) would be to consider these models' behavior for a *networked* popula-

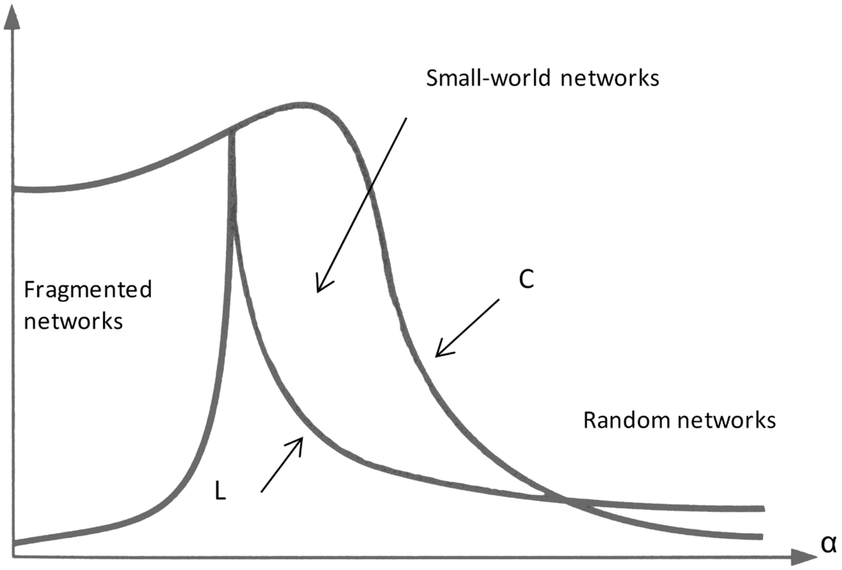

Figure 3. Path length as a function of alpha: at the critical alpha value, many small clusters join to connect the entire network, whose length then shrinks rapidly. The region between the curves, where path length, L. is small and clustering coefficient, C. is large represents the presence of small world networks (redrawn after Watts 2003: 81).

tion of individuals.

Human social networks have been the subject of a considerable amount of interest in recent years, with special attention being paid to their distinctive 'small world' or 'six degrees of separation' structure. In a 'small-world' network, path length (the 'distance', or number of intervening points between any two 'nodes') is small and 'clustering' (the tendency of 'nodes' to form small, dense groups) is large (Figure 3; Buchanan 2002; Watts 2003). The formation of small-world networks is thus a function of the probability of 'nodes' being connected outside of their immediate group Tellingly, Watts (2003: 76–77) describes a 'world' in which clustering is high and inter-cluster connectivity low as a 'caveman' world. Here, although path length between individuals is certainly low, this is because individual groups are so small. In contrast, where there is a high probability of individuals forming connections with others from outside their immediate group, relations are loose and extended and path length small because nodes are closely connected throughout the system (Watts 2003: 76–77).

In the small, densely clustered groups characteristic of the so-called 'caveman' world, interactions occur repeatedly between the same individuals, resulting in 'dense encounter sets' (Hillier and Hanson 1984). The patterns of social interaction in such societies are primarily (if not solely) organized around kinship and close physical proximity (Whitelaw 1991: 182; see also Lofland 1973; Wilson 1988). However, as the number of individuals in any group increases, the number of inter-individual relationships possible increases exponentially (Whitelaw 1991: 182) and larger groups inevitably become less dense 'encounter sets' (Hiller and Hanson 1984: 27), meeting one another less frequently, and the combination of increased numbers and less frequent encounters incurs significant cognitive costs (Dunbar 1992a, 1993, 2003; Gamble 1999; Roberts 2010; Watts 2003). Larger group sizes, then, are costly. However, even in these larger societies there will be groups of kin or individuals whose close physical proximity results in frequent intimate and personal interactions and mutual knowledge, and Kudo and Dunbar (2001: 10) argue that larger groups are created not simply by having larger coalitions (as coalition size does not increase isometrically with group size) but rather by connecting more coalitions together via weak links between the dense clusters of closely-linked individuals. Thus human-scale 'small worlds' are created out of large aggregations . It is these processes that impact so significantly on the spread of innovation.

Multivariate studies of innovativeness among rural communities (Lewis 1979: 287) highlight the relevance of network structure to the dissemination of novelties. The principal dimension referred to is the number of individual contacts beyond the immediate neighbourhood: 'new' information or cultural innovation tends to come through weak links to individual outside an immediate 'strong' social circle (Granovetter 1973, 1983). A secondary dimension refers to attitudes towards change, and is cross-cut by a variety of other biological and socioeconomic factors including age—in these studies the younger were more dissatisfied with the status quo, and thus more open to the adoption of innovations, although Reader and Laland's (2001) meta-analysis of the primate data suggested that rates of innovation were higher among adults than among juveniles (see also Kendal et al. 2005; Kyriacou and Bruner this volume). The third dimension relates to degrees of leadership and respect within communities and the role of such individuals in receiving novel influences and acting as hubs to disseminate them among fellow members of local communities—information flow is faster, more credible, and more influential along strong ties (Buchanan 2002; Granovetter 1973, 1983). As Cullen's Cultural Virus Theory predicts, then, innovations cannot disseminate as far in a ‘caveman’ world of discrete social clusters as in a world of loose, extended linkages. It is weak ties that are associated with new information, innovation, and decision-making and thus with rapid cultural change.

As yet, however, study of prehistoric social networks remains limited and mainly has been applied to island contexts such as the Pacific islands (Hage and Harary 1991), the Aegean archipelago (Broodbank 2000; Brughmans 2010; Evans et al. 2009) and Viking Scandinavia (Sindbaek 2007a, b). In a social network approach sites (or islands) become nodes and connections between them edges, forming a simple graph. Refinements include adjusting for the significance of nodes (based on, for example, inferred population size derived from carrying capacity/island size), and/or for the different lengths of edges between vertices (corresponding not only to distance but to ease of traversing them given contemporary transportation technologies). Such techniques offer considerable potential for the investigation of the character of prehistoric societies in robust quantitative terms which allow consideration of social change over time (e.g., Coward 2010).

INNOVATION IN HETEROGENEOUS SOCIAL GROUPS

However, individuals in a population also differ in much more fundamental ways than simply in terms of their positioning and connectivity in social networks. Firstly, and most obviously, individuals differ biologically. Age and gender, for example, have significant effects on the kinds of skills people are cognitively and physically able to devise and/or to learn and practice. They also may be significant in terms of the positioning of individuals within social networks, and hence the cultural transmission of behaviors. For example, as already noted among the Gombe chimpanzees, infants or juveniles ‘are the most likely candidates for stumbling upon a new tool-using technique’ (Goodall 1986: 563), although this may not extend to other primates (Reader and Laland 2001). It has also been claimed that the ‘social brain’ hypothesis may apply more strongly to females than to males as their need to keep track of social interactions is greater, resulting in sexually divergent selective pressures (Lindenfors 2005: 407). Interestingly, males and females seem to play different roles in primate social networks, with males acting as links between tightly-bonded female cliques rather than comprising cliques of their own (Kudo and Dunbar 2001). Among primates generally, males are more likely to innovate than females, although female chimpanzees were more likely to use tools at Gombe (though, as Goodall points out [1986], this could simply be a reflection of the fact that they spend more time feeding on those foods that require tools to extract).

In fact, heterogeneity of individuals within societies also may be of adaptive benefit more generally. As discussed above, the payoffs between species-wide strategies of social learning and individual trial-and-error learning are clearly hugely influenced by environmental variability, but within species strategies may also vary *within* populations. Selection often results in genetic uniformity, but balancing selection or selection in fluctuating environments may maintain phenotypic polymorphisms (Keller and Miller 2006). For example, left-handedness is heritable and therefore under selection, but despite being associated with various developmental disorders and reduced fitness has apparently persisted at low rates of 10–13% since at least the Neolithic (Raymond et al. 1996: 1627) and probably longer (Steele and Uomini 2005). It is believed this may be due to the advantage of surprise enjoyed by left-handers when they engage in combat with the majority of right-handers (Faurie and Raymo 2005; Raymond et al. 1996: 1628).

This kind of frequency-dependent selection also may be behind some aspects of cognitive variability; for example, it may explain the low but persistent rates of occurrence of psychopathy among human populations (roughly 3% in males and 1–2% in females; Colman and Wilson 1997; Pitchford 2001). Psychopathy appears to be largely, if not solely, genetic (Pitchford 2001: 7), and game-theoretic sociobiological models suggest that the habitual use of manipulative and predatory social interactions is highly adaptive—but only for a small minority (Colman and Wilson 1997: 6; Mealey 1995: 524, cited in Pitchford 2001).

In short, individual variation within a population may represent something more interesting than simply neutral variation around an adaptive average. Many within-species behavioral differences are strongly related to fundamental biological factors such as age and/or sex, but in many species individuals also show other significant differences in behavioral styles that go beyond context-dependence (Dall et al. 2004). The adaptiveness of such differences in what is termed ‘personality’ among humans (‘coping styles,’ ‘behavioral tendencies/strategies,’ etc., is preferred for non-human animals) is by no means universally accepted. Many see personality as nothing more than ‘a product of selection-irrelevant genetic variation, the random effects of sexual recombination, and non-adaptive phenotypic plasticity in response to environmental differences in development’ (Tooby and Cosmides 1990, cited in Figueredo, Vásquez et al. 2005: 1350; see also Figueredo, Sefcek et al. 2005: 851).

However, there are several reasons to believe that personality differences are under genetic control and under selection; behavioral tendencies strikingly similar to the human five-factor model (FFM) of personality traits (openness, conscientiousness, extraversion, agreeableness, neuroticism) can be generalized across a wide variety of contexts and species, from primates to insects (Dall et al. 2004: 735; Figueredo, Sefcek et al 2005: 858). In addition, there are correlations between personality traits and genetics, as well as longevity, fertility, mate choice, and personality traits which suggest that personality traits *cannot* be adaptively neutral (Figueredo, Sefcek et al. 2005, 863; Figueredo, Vásquez et al. 2005, 1351). In fact, it has been suggested that ‘the genetic variation underlying individual differences allows species with differentiated personalities to occupy a diverse range of social and environmental niches’ (MacDonald 1998: 142). The classic hawk-dove model beloved of

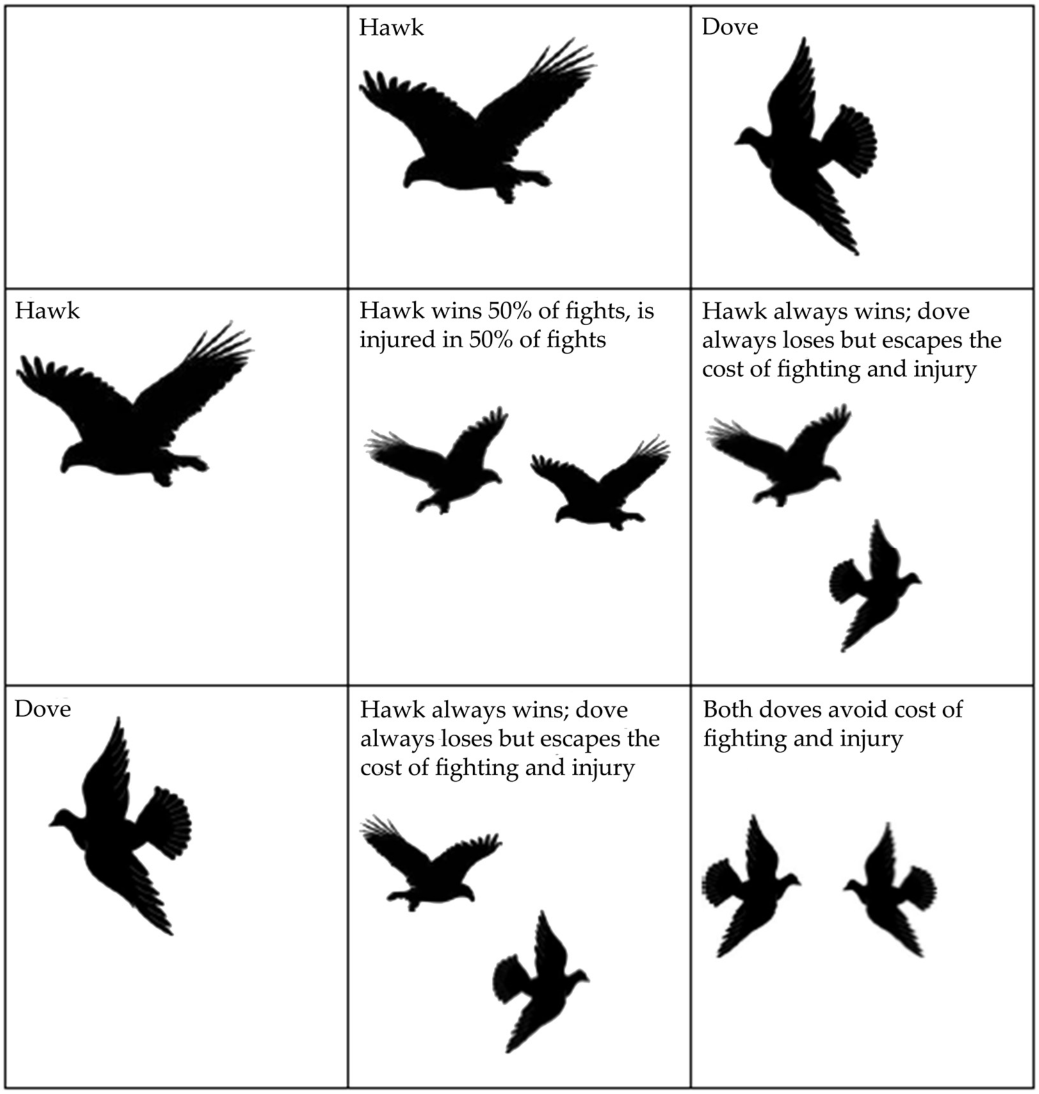

Figure 4. Two polymorphic types co-exist in a species: in situations of confrontation 'hawks' always attack, sustaining the cost of fighting, but potentially achieving victory; 'doves' always retreat, avoiding the costs of fighting and potential injury but never achieving victory (redrawn after the Encyclopedia Britannica, Inc. 2007).

game theory (Figure 4) provides a good example of some of the mechanisms via which stable polymorphic 'types' can co-exist in species; to reach an evolutionarily stable strategy (ESS) 'each individual can perform actions randomly with fixed probabilities and thus generate the predicted mix of strategies in large populations, or fixed proportions of individuals can play each strategy consistently' (Dall et al. 2004: 735). This latter scenario could underpin the development of personality types, particularly if models allow for 'eavesdropping' (i.e., allowing players the cognitive ability to predict one another's actions based on observations of their past behavior—essentially, granting them ToM or at least a sophisticated form of social cognition). The ability to 'eavesdrop' appears to select for consistent individual differences in aggression, and thus polymorphic populations (Dall et al. 2004: 736).

Evolution of behavioral 'specialists' within species may seem contrary to an overall pattern of selection for behavioral *flexibility* over fixed, heritable strategies among hominins (Keller and Miller 2006: 21). However, it is worth pointing out that there are also costs to flexibility, notably the extent to which it increases the chances of responding inappropriately (Keller and Miller 2006: 737). The canalizing effect of personality types on behavior may be compensated for by the variety resulting from the many potential combinations of individual personality traits within and between individuals and also with life history variables such as sex and age. For example, male/female correlations along the various dimensions of the FFM suggest a (statistical) bias along the lines of that suggested by reproductive fitness theory, whereby males score higher on social dominance, sensation seeking, extraversion, and risk taking and females on nurturance/love scales. Further, these 'sex differences in behavioral activation systems are ... maximal during late adolescence and early adulthood', at precisely the individual reproductive potential peak (Figueredo, Vásquez et al. 2005: 854), further evidence for the adaptiveness of personality traits.

Such rich individualism appears to be characteristic only of social species, however (Figueredo, Sefcek et al. 2005: 856), suggesting that individual variation along personality dimensions might be adaptive primarily in social competition. Certainly most terms used to describe the FFM personality traits are objective evaluations that 'reflect observer evaluations of others as potential contributors to, or exploiters of, the group's resources' (Figueredo, Sefcek et al. 2005: 853), leading McAdams(1992: 329) to describe the FFM as a 'psychology of the stranger' in recognition of its ease of assessment in new acquaintances. It has been argued that the evolution of cooperation and sharing may depend on individuals in a group having varying tendencies to altruism (Dall et al. 2004: 736), and by influencing individual social relationships, greater individual distinctiveness also might be adaptive in terms of its impact on the relative clustering and density of networks—for example, through the 'birds of a feather' effect whereby like-minded individuals group together, thus facilitating the formation of those all-important 'weak links' across local family / geographically-structured groups and allowing the rapid dissemination of new ideas and adaptive innovations, as well as information, resources, etc. It is possible, therefore, that among hominins selection for larger group sizes and extended social networks also created an environment in which the maintenance of multiple polymorphisms for personality types facilitated teamwork and communal effort, which requires a division of labor in which different subtasks are performed in co-ordination (Anderson and Franks 2001: 534). While the evidence remains sketchy and anecdotal, management theory suggests that the optimal configuration of a team comprises between five and eight different complementary 'types' of people (Barrick and Mount 1991; Belbin 1981). Clearly more research needs to be done in this area, but the maintenance of high levels of personal heterogeneity within groups may well prove to be a significant biosocial innovation associated with hominization.

CONCLUSIONS

Traditionally, the concept of innovation in human evolution has focused on innovation in material culture and technology. However, in its broadest sense as simply 'something new,' hominization involves many innovations, not solely technological, but also biological, social, and cultural. In-depth study of individual aspects of human evolution—encephalization, life-history strategies, subsistence, technology, social structure—has yielded valuable information. However, these factors cannot be teased apart in any straightforward way, and none are readily identifiable as 'prime movers.'

We have covered a great deal of ground in this paper, and there are no easy conclusions. However, a number of generalizations can be drawn from the preceding discussions regarding how archaeologists and paleoanthropologists should study innovation.

Of paramount importance is the need to broaden the consideration of innovation from a narrow technological definition to embrace the bio-eco-socio-behavioral context of technological development. Having argued throughout this paper against oversimplification, we do acknowledge that the current state of the art in archaeology does not allow—and may never allow, given the vagaries of archaeological preservation—for the consideration of many of the more contingent historical and psychological factors impacting on prehistoric decision-making and the resulting pattern of the archaeological record. However, while some form of simplification for analytical purposes will always be necessary, we have discussed above some of the major methodologies for modelling the production and dissemination of innovation, which represent interesting points of departure for modelling these processes in their wider contexts. Some of these are relatively well known to archaeologists (though still often neglected) and others have emerged in recent literature and are now ripe for exploitation, recognizing as they do the complexities of interdependencies between factors which are too often separated out in an oversimplified manner. A much fuller picture of hominin and human evolution emerges when we accept the possibility of complex interrelationships and dynamic feedback loops between the different variables through which, for example, a modified life history strategy may be both an innovation in itself as well as a facilitator of subsequent innovative behaviors in distinct domains.

In this paper we have discussed many innovations and the factors which promote and maintain them, from the macro-scale of climatic and environmental effects to the micro-scale of social networks and personality types. Our aim throughout has been to highlight the interdependence of these multiscalar innovations and the factors influencing them, and to draw out some of the many correlations that form the complex constellations of biological, technical, social, and behavioral strategies pursued by individuals, groups and populations in hominin evolution. It appears that no straightforward relationships exist between innovation, intelligence, and encephalization, and a much more plausible explanation for their co-occurrence in human evolution situates innovation and behavioral flexibility in evolutionary context. The variability of these environments—and the amplitude/frequency of that variability—are significant factors in determining the adaptiveness or otherwise of potentially costly behavioral flexibility, especially directly in subsistence/foraging contexts. However, the mechanisms by which behavioral flexibility is translated into innovation occur primarily at the level of the social group and are part and parcel of a range of other hominin social adaptations, including significant shifts in life history scheduling, and concomitant changes to social lives resulting from increasingly cooperative breeding. These developments provide the framework within which archaeological study of innovation (indistinguishable on prehistoric timescales from dissemination) must proceed, as it is the increasingly complex intra-group social structures caused by increasing individual heterogeneity and distinctiveness, that determine (and that may have evolved to facilitate) the development, spread, and maintenance of innovations in material culture and the behaviors surrounding them.

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