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THE NICHE CONSTRUCTION PERSPECTIVE:
Implications for evolution and human behaviour

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Abstract. The vibrancy of the field of evolution and human behaviour belies the fact that the majority of social scientists are deeply unhappy with evolutionary accounts of human behaviour. In part, this reflects a problem within evolutionary biology: neo-Darwinism fails to recognize a fundamental cause of evolutionary change, “niche construction”, by which organisms modify environmental states, and consequently selection pressures, thereby acting as co-directors of their own, and other species’, evolution. Social scientists are rarely content to describe human behaviour as fully determined by naturally-selected genes, and view humans as active, constructive agents rather than passive recipients of selection. To be aligned with this viewpoint, evolutionary biology must explicitly recognize the changes that humans bring about in their world to be drivers of evolutionary events. Learning and culture have played important evolutionary roles, by shaping the pattern and strength of selection acting on our ancestors. The incorporation of niche construction as both a cause and a product of evolution enhances the explanatory power of evolutionary theory and provides what ultimately will prove to be a more satisfactory evolutionary framework for understanding human behaviour. Here we spell out some of the important implications of the niche-construction perspective for the field of evolution and human behaviour.

Keywords: evolution, niche construction, natural selection, evolutionary psychology, human behavioural ecology

INTRODUCTION

The human genome has now been sequenced, and attention has moved on to secondary analyses of the data that have come out of the project. One such set of

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analyses are attempts, by mathematically-minded geneticists, to detect statistical signatures in the genome of recent, rapid selection – genes favoured by natural selection over the last 100,000 years (WANG et al. 2006; VOIGHT et al. 2006). While relatively sensitive statistical tests for positive selection have been developed, such methods are in their infancy, and far from perfect: they do not, for instance, detect such genes that have gone to fixation (WANG et al. 2006). Nonetheless, thus far, such analyses reveal nearly two thousand human genes that show signals of very strong and recent selection, including alleles that provide resistance to diseases such as malaria, and alleles that allow the metabolism of lactose in cows milk. One of the more intriguing categories, highly-represented (> 15%) in inferred selective events, is neuronal function (WANG et al. 2006), including the serotonin transporter (*SLC6A4*), glutamate and glycine receptors (*GRM3*, *GRM1*, and *GLRA2*), olfactory receptors (*OR4C13* and *OR2B6*), synapse-associated proteins (*RAPSN*), and a number of brain-expressed genes with largely unknown function (*ASPM*, *RNT1*). In other words, a striking proportion of recently favoured genes are expressed in the human immune system and brain.

Humans possess approximately 40,000 genes, so researchers should not be surprised that a small proportion (currently c. 5%) show signs of recent positive selection. Yet the dominant view within (especially North American) evolutionary psychology has been that our species has undergone comparatively little evolutionary change in recent millennia, particularly with respect to mental adaptations, which were regarded as products of resistant-to-change gene complexes (COSMIDES and TOOBY 1987; see LALAND and BROWN 2002, for an overview). The large numbers of human genes now known to have been subject to recent positive selection, including those expressed in the brain, are an embarrassment to this evolutionary psychology viewpoint.

However, copious signs of recent positive selection do make sense when one considers the dramatic changes in selection pressures that our species has experienced. Amongst other challenges, in the last 100,000 years humans have:

- spread from East Africa around the globe,
- experienced an ice-age,
- begun to exploit agriculture,
- witnessed rapid increases in densities,
- experienced a new proximity to animal pathogens.

What is immediately striking about these major challenges is that all but one (the ice-age) have been self-imposed: that is, human activities have modified selection pressures, for instance by dispersing into new environments with different climatic regimes, devising agricultural practices, or domesticating livestock. These activities are instances of human ‘niche construction’ (the modification of environments by organisms), which, we claim, have precipitated evolutionary responses in the human genome. The capacity for culture is clearly an important factor underlying the potency of human niche construction: agriculture was not independently invented by each farmer, nor is its presence an unlearned maturational outcome of human gene expression. Moreover, even in the case of climatic regimes, beyond human control, human 'cultural niche construction' would have strongly affected the intensity of selection, for instance, by manufacturing clothes or shelters, or controlling fire. Human cultural niche construction has been a co-director of recent human evolution. This is essentially the conclusion reached by the geneticists analysing the genome:

> Homo sapiens have undoubtedly undergone strong recent selection for many different phenotypes…. Given that most of these selective events likely occurred in the last 10,000–40,000 years…it is tempting to speculate that *gene-culture interactions directly or indirectly shaped our genomic architecture* (WANG et al. 2006, *PNAS* p140, our italics).

The same conclusion was reached by pioneers of the field of 'gene-culture co-evolution' some 25 years ago (LUMSDEN and WILSON 1981; FELDMAN and CAVALLI-SFORZA 1981; BOYD and RICHERSON 1985; see LALAND and BROWN 2002, for an overview). These researchers view genes and culture as two interacting forms of inheritance, with offspring acquiring both a genetic and a cultural heritage from their parents and other conspecifics. Their mathematical models have shown how our views of human evolution change when both inheritance systems are taken into account (RICHERSON and BOYD 2005). In this article, we suggest that attempts to understand how genes and culture co-evolve require the concept of 'niche construction'. We then discuss the implications of taking a niche-construction perspective on research in the human sciences and evolutionary psychology.

NICHE CONSTRUCTION

Niche construction is the very general process whereby organisms modify their own and/or each others' niches, through their metabolism, their activities, and their choices. It is far from restricted to humans: numerous animals manufacture nests, burrows, holes, webs and pupal cases; plants change levels of atmospheric gases and modify nutrient cycles; fungi and bacteria decompose organic matter; bacteria fix nutrients (LEWONTIN, 1982, 1983; ODLING-SMEE, 1988; ODLING-SMEE et al. 2003). The defining characteristic of niche construction is not organism-driven modification of the environment per se, but rather the modification of the *relationship* between an organism and its environment (ODLING-SMEE 1988), and hence niche construction subsumes habitat selection, dispersal and migration.

Advocates of the niche-construction perspective within evolutionary biology stress the active role that organisms play in driving evolutionary and co-evolutionary events. They seek to explain the adaptive complementarity of organism and environment in terms of dynamic, reciprocal interactions between the processes of natural selection and niche construction. Evolution thus entails networks of causation and feedback in which previously selected organisms drive environmental changes, and organism-modified environments subsequently select for changes in organisms.

Niche-construction theory differs from conventional conceptualisations of evolution in which, leaving aside complications such as co-evolution and habitat selection, adaptation is a process by which natural selection shapes organisms to fit pre-existing environmental templates. The causal arrow points in one direction only: environments are the source of selection, and they determine the features of living creatures. According to GEORGE WILLIAMS (1992, p.484): “Adaptation is always asymmetrical; organisms adapt to their environment, never vice versa”.

The conventional stance is based on some metaphysical assumptions that have underpinned evolutionary thought since the Modern Synthesis, including ERNST MAYR’S (1961) distinction between proximate and ultimate causes. For Mayr, developmental processes could not be regarded as independent causes of evolutionary events, since their characteristics, including their ability to control and constrain, are themselves fully explained by prior natural selection. If developmental processes direct evolutionary events, this is only the *proximate* manifestation of the *ultimate* cause of natural selection; conversely, those aspects of development that have not been shaped by selection play no evolutionary role. Mayr was extremely influential in bringing this commonly made distinction between ‘proximate’ and ‘ultimate’ causes to prominence within biology. Mayr argued that natural selection should be regarded as the *ultimate* cause of phenotypic characters (AMUNDSON 2005), thereby effectively devaluing so-called proximate causes as explanatory tools within evolutionary biology.

As niche construction includes developmental processes, Mayr’s stance, which is widely accepted, also prevented evolutionary biologists’ from recognising niche construction as an evolutionary process in its own right (LALAND and STERELNY 2006). Instead, niche construction is perceived to have no *independent* evolutionary significance because, to the extent that it is evolutionarily consequential, it is fully explained by a preceding “cause” or “process”, namely preceding natural selection (DAWKINS 2004). Niche-construction effects are merely extended phenotypes, and extended phenotypes play the same role in evolutionary biology as ordinary phenotypes, namely to affect the replication potential of the alleles contributing to those phenotypic effects (DAWKINS 2004). While this stance recognizes that modification of the selective environment does occur, it does not view such environmental modification as a process with any causal significance in evolution. Rather, to the extent that niche construction instigates evolutionary events, such events are attributed to prior selection for niche construction.

There are major problems with this line of reasoning (ODLING-SMEE et al. 2003; LALAND and STERELNY 2006), the most obvious being that not all evolutionarily consequential niche construction is under genetic control. This is self-apparent for humans, where it is clear that genetic variation explains only a fraction of behavioural variation. Consider the case of human lactose absorption.

Adult humans vary in their ability to consume dairy products without sickness as a result of physiological differences in the activity of the enzyme lactase, which relate to genetic variation (DURHAM 1991). A strong correlation exists across cultures between the presence of the genes for lactose absorption and a history of dairy farming (ULIJASZEK and STRICKLAND 1993). This has led to the hypothesis that dairy farming constructed the selection pressures that led genes for lactose absorption to become common in pastoralist societies. Theoretical analyses provide strong support for this hypothesis and confirm that dairy farming spread before the genes for lactose absorption, not the other way around (AOKI 1986; FELDMAN and CAVALLI-SFORZA 1989; HOLDEN and MACE 1997). Dairy farming is apparently an instance of human cultural niche construction that is mediated by cultural processes. There are no genes for dairy farming (using "genes for" in the sense of DAWKINS 1976). Genes do not constitute the appropriate level of analysis to explain why individuals in only some societies farm cattle - this is a cultural phenomenon. Yet in spite of the fact that dairy farming is not caused by genes and is not a product of natural selection, it has clearly had evolutionary consequences. There are many such examples (ODLING-SMEE et al. 2003).

The niche-construction perspective differs from the conventional one in recognizing two major adaptive processes in evolution, natural selection and niche construction, and two general forms of inheritance, genetic and ecological inheritance (ODLING-SMEE 1988). Ecological inheritance refers to the modified environments (e.g. nests, burrows), incorporating modified selection pressures, that descendant organisms inherit from their ancestors. Organisms transmit to their offspring, and subsequent descendents, physically altered selective environments, both through actions on their biological and non-biological environments, and by their habitat choices.

Many researchers have explored the evolutionary ramifications of niche construction by developing and analyzing mathematical models (LALAND et al. 1996, 1999, 2001; ODLING-SMEE et al. 2003; IHARA and FELDMAN 2004; SILVER and DI PAOLO 2006; BORENSTEIN et al. 2006). All such analyses conclude that niche construction is evolutionarily consequential. In some cases, population genetic models investigate the dynamics of the joint evolution of environment-altering, niche-constructing traits in organisms and 'recipient traits', whose fitness depends on feedback from natural selection in environments that can be altered by niche construction (LALAND et al. 1996, 1999, 2001; ODLING-SMEE et al. 2003).

Through their niche construction organisms change their local environment, modifying the pattern and strength of selection acting on their population. The theoretical analyses suggest that this "self-imposed" selection resulting from niche construction will often override external sources of selection (that is, selection acting on the population independent of their niche-constructing activities) to create new evolutionary trajectories, which lead to the fixation of otherwise deleterious alleles, the support of stable equilibria where none are expected, and the elimination of what would otherwise be stable polymorphisms. Even niche construction that only weakly affects resource dynamics can significantly alter both ecological and evolutionary patterns. This is because traits whose fitness depends on alterable sources of selection co-evolve with traits that alter sources of selection. Such coevolution results in evolutionary dynamics that are very different from what would occur if each trait had evolved in isolation. Other theoretical studies corroborate and extend these findings. Amongst the most significant of these is SILVER and DI PAOLO'S (2006) finding that niche-construction traits can drive themselves to fixation by simultaneously generating selection that favours 'recipient' trait alleles and linkage disequilibrium between niche-construction and recipient trait alleles.

While most theoretical treatments of niche construction have focused on the selection to which an organism is exposed, DONOHUE (2005) discusses how niche construction can also influence the expression of phenotypic and genetic variation. DONOHUE (2005) and DONOHUE et al. (2005) showed experimentally how niche construction frequently occurs in plants through developmental plasticity, allowing them to determine the selective environments that they or their offspring experience. For instance, seed dispersal ability frequently influences the competitive environment experienced by seeds, seedlings and adult plants. Flowering time strongly affects the seasonal environment that the seeds experience. Germination timing effectively involves habitat choice in plants, since certain environmental conditions must be present to break dormancy and additional environmental conditions must be present to enable germination after dormancy is broken. For these reasons, it is reasonable to regard traits such as seed dispersal ability, flowering time and germination timing as niche-constructing traits. Donohue also described an experimental study with *Arabidopsis thaliana* showing how two niche-constructing traits – flowering and germination time – influence selection, phenotypic expression and genetic variation, resulting in novel life-history expression, and accounting for variation between spring and winter annual life histories (DONOHUE 2005).

Mathematical analyses also suggest that ecological inheritance (ODLING-SMEE 1988; ODLING-SMEE et al. 2003) can generate unusual evolutionary dynamics. Frequently, the evolution of the recipient trait depends on the frequency of the niche-constructing trait over several generations. Theoretical population genetic models have established that processes that carry over from past generations can change the evolutionary dynamic in a number of ways, generating time lags in response to selection of the recipient trait, momentum effects (populations continuing to evolve in the same direction after selection has stopped or reversed), inertia effects (no noticeable evolutionary response to selection for a number of generations), opposite responses to selection, and sudden catastrophic responses to selection (FELDMAN and CAVALLI-SFORZA 1976; KIRKPATRICK and LANDE 1989; LALAND, ODLING-SMEE and FELDMAN 1996, 1999, 2001; ROBERTSON 1991; WOLF, BRODIE and WADE 2000; WOLF et al. 1998).

Niche construction provides a non-Lamarckian route by which acquired characteristics can influence the selective environment. Acquired characteristics are of particular significance to vertebrate evolution. The Galapagos woodpecker finch provides an example (ODLING-SMEE et al. 2003). These birds create a woodpecker-like niche by learning to use a cactus spine or similar implement to peck for insects under bark (TEBBICH et al. 2001), creating selection pressures that favoured a bill able to manipulate tools rather than the sharp, pointed bill and long tongue characteristic of most woodpeckers. While the information acquired by individuals through ontogenetic processes cannot be inherited because it is lost when they die, processes such as learning can nonetheless still be of considerable importance to subsequent generations because learned knowledge can guide niche construction in ways that do modify natural selection.

This route is considerably enhanced by social learning, which allows animals to learn from each other. Hundreds of species of mammals, birds and fishes are now known to learn socially (ZENTALL and GALEF 1988; HEYES and GALEF 1996), allowing novel learned traits to sweep through populations, and exposing individuals to novel selection pressures. There is already considerable interest among evolutionary biologists in the role that imprinting, song learning, habitat imprinting, cultural transmission and various other forms of learning play in speciation, the evolution of adaptive specializations, adaptive radiations, the colonization of new habitats, brood parasitism and sexual selection in vertebrates (AOKI et al. 2001; BELTMAN 2003, 2004; LALAND 1994; KIRKPATRICK and DUGATKIN 1994; ten CATE and BATESON 1988; ten CATE 2000; WEST-EBERHARD 2003). From the niche-construction perspective, learning in general, and social learning in particular, is likely to exert a widespread influence on animal evolution. The significance of acquired characters to evolutionary processes is further amplified with stable trans-generational culture, and it is now widely believed that such characters were probably important to hominid evolution (CAVALLI-SFORZA and FELDMAN, 1981; RICHERSON and BOYD 2005). For instance, theoretical analyses by LALAND et al. (2001) explored the evolutionary consequences of cultural niche construction. They revealed circumstances under which cultural transmission could overwhelm natural selection, accelerate the rate at which a favoured allele spreads, initiate novel evolutionary events, and possibly trigger hominid speciation. In fact, the analyses found that, because cultural processes typically operate faster than natural selection, cultural niche construction is likely to have more profound consequences than gene-based niche construction.

In summary, there is now strong theoretical and empirical support for the argument that niche construction affects the process of evolution. Such studies refute any suggestion that niche construction can be neglected because it is intractable or inconsequential. The analyses imply that population genetic models that ignore niche construction will frequently generate inaccurate predictions and misleading findings. Niche construction changes the evolutionary process in fundamental ways, by creating an ecological inheritance, by modifying phenotypes, norms of reaction and heritabilities, and by allowing acquired characters to play a significant role in evolution.

Ramifications for the human sciences

ODLING-SMEE et al. (2003) identify two principal reasons why most human scientists find it difficult to make use of evolutionary theory. One is that standard evolutionary theory appears to have too little to offer them. Human scientists are predominantly interested in human behaviour and culture, rather than genes, and as a consequence they have little use for evolutionary theory. The second is that the adaptationist accounts derived from standard evolutionary theory, for example in evolutionary psychology, are regarded by the majority of human scientists as simplified to the point of distortion.

There are two barriers to integration. The first is that standard evolutionary theory recognises only a single role for phenotypes in evolution: diverse phenotypes survive and reproduce differentially in the face of selection and chance, the fittest passing on their genes to the next generation. Second, standard evolutionary theory recognises only a single evolutionarily significant inheritance system, genetic inheritance. This recognizes that human developmental and cultural processes, including cultural inheritance, contribute to human variation, and therefore to the diversity of human phenotypes subject to selection, but it does not recognize that human cultural processes affect human evolution in any other way. These restrictions minimize the role of developmental and cultural processes in human evolution.

Niche construction removes both these restrictions. It removes the first because niche-constructing phenotypes also construct and modify components of their environments, and in doing so they modify some of the natural selection pressures in their environments that later act as sources of selection on them, and their descendents. It removes the second restriction because niche-constructing phenotypes generate a second general inheritance system in evolution, ecological inheritance. In humans, cultural niche-construction contributes directly to ecological inheritance.

In practice, all complex organisms gain the information that guides their niche-constructing activities through several processes including population genetics, ontogenetics, and in humans, cultural processes. Niche construction is potentially guided by semantic information from all the information stores carried by phenotypes, but only genetic information is an obligate influence on niche construction. That is, in every species, niche construction is informed by naturally-selected genes, in most it is also informed by ontogenetic processes, for example, learning in animals, while in humans, and a few other species, it is informed by cultural processes as well. Human phenotypes therefore typically depend on genetic, ontogenetic, and cultural processes operating at distinct, but richly interconnected levels (ODLING-SMEE 2006).

Mathematical analysis has demonstrated that cultural niche construction, guided by culturally transmitted information, is a particularly potent modifier of environments, with major evolutionary and genetic consequences both for humans, and other species in shared ecosystems (LALAND et al. 2001; IHARA and FELDMAN 2004; BONI and FELDMAN 2005). These analyses suggest that cultural processes can amplify the evolutionary feedback loop that is generated by niche construction (LALAND et al. 2001; ODLING-SMEE et al. 2003). Human evolution may also be unique in that our cultural capacities, and our cultural niche constructing activities, apparently reinforce each other. Trans-generational cultural niche construction modifies environments in ways that favour ever-more culture, causing cultural niche construction to become ever-more powerful (LALAND et al. 2000; ODLING-SMEE et al. 2003; STERELNY 2003; TOMASELLO et al. 2005). SILVER and DI PAOLO'S (2006) observation that niche construction can be self-reinforcing, with niche constructing traits driving themselves to fixation, could be particularly relevant to human evolution. Niche-constructing and cultural capabilities may have 'run away' together, in a dynamic strikingly akin to Fisherian runaway sexual selection (LALAND et al. 2000).

Niche construction theory may be particularly relevant to the dynamics of cultural traits as the theory can incorporate the effects of the cultural background as a form of constructed niche. This is illustrated by a series of theoretical studies of fertility control and the demographic transition. For instance, IHARA and FELDMAN (2004) examined the effects of a preference for a high or low level of education on the evolution of small family size. They assumed that the average level of education may affect the degree to which traits are transmitted obliquely rather than vertically, for example, from teachers rather than parents to pupils. They found that a preference for small family size can evolve if individuals with few offspring are more likely to transmit their fertility preference to the offspring generation than individuals with a high number of offspring. Similar dynamics relating the education and fertility preference traits were also found under the assumption that the average level of education influences the rate of horizontal transmission of the use of fertility control (KENDAL et al. 2005). Here, cultural niche construction facilitates the spread of the use of fertility control, where otherwise fertility selection and conformity would prevent the spread of this trait when rare. Both studies revealed the classic niche-construction characteristic of a time-lag between the increase in the average level of education and subsequent decline in fertility; a pattern that is consistent with, and may partially explain, a typical demographic transition. BORENSTEIN et al. (2006) developed a metapopulation cultural niche construction model where the frequency of a trait, such as the preference for a high level of education, affects the construction of a social interaction network, through which other cultural traits may percolate. They found that local between-population cultural niche construction could account for the spread of reduced fertility preference across countries at ever lower levels of development (BONGAARTS and WATKINS 2005).

Another system that exhibits feedback between human cultural niche construction and genetic selection is the host-parasite relationship between antibiotic treatment and viability selection for antibiotic-resistant bacterial strains. This is an example of inter-specific cultural niche construction. BONI and FELDMAN (2005) found that the cultural transmission of antibiotic use favours selection of resistant bacterial strains, which in turn can result in cultural selection for the avoidance of antibiotic use. This kind of host behaviour can result in the classic niche-construction phenomenon of maintaining strain polymorphism even in parameter regions where it would not otherwise be expected. Interestingly, the evolution of either the host activity or the parasite strain can be viewed as a niche-constructive activity that modifies the selective environment of the other. Potentially this promotes an arms race between two types of transmitted information, cultural and genetic. Here, the niche constructive effects can be described fully in terms of trait-trait co-evolution as there is no ecological inheritance of a constructed 'resource' that is separate from the cultural or the genetic information transmission systems. The relative frequencies of bacterial resistance and sensitivity are the effective 'resource' influencing the cultural evolution of antibiotic treatment, and visa versa.

In summary, theoretical population genetics analyses provide strong support for the hypothesis that human cultural niche construction is likely to be evolutionary consequential, driving evolutionary events in our own species and also in those species with which we interact. Such analyses potentially help to make sense of some puzzling phenomena in the human sciences, such as the demographic transition.

THE ADAPTIVE LAG HYPOTHESIS

A dominant assumption within the field of evolutionary psychology is that the human mind is made up of psychological mechanisms that have evolved in response to selection pressures faced in the past by our hominid ancestors. For instance, COSMIDES and TOOBY (1987, p. 280–1) stated that 'The recognition that adaptive specializations have been shaped by the statistical features of ancestral environments is especially important in the study of human behavior … Human psychological mechanisms should be adapted to those environments, not necessarily to the twentieth-century industrialized world'. The past environment in which selection apparently forged human psychology is generally referred to as the 'environment of evolutionary adaptedness' and has been characterised as an African savannah habitat (COSMIDES and TOOBY 1987). Evolutionary psychologists often stress how the environments experienced by contemporary human populations differ hugely from those experienced by our ancestors, for instance containing modern housing, transportation and medical interventions. The mismatch between current and past environments is argued to produce an 'adaptive lag', such that human behaviour shows an adaptive fit to past, but not current, environments.

Selection pressures on genes that underlie our mental architecture are assumed to be unable to keep up with the rapidly changing environment that has been brought about by human innovation and technology.

This account differs greatly from the views of many human behavioural ecologists, who investigate whether observable human behaviour can be explained in terms of flexible, adaptive response to local environmental and social conditions (BORGERHOFF MULDER 1990). The optimality models used by these researchers begin with the assumption that the flexibility of human behaviour will produce optimal strategies to cope with specific, current conditions. Human behavioural ecologists focus their research on small-scale populations, perhaps suggesting that they are expecting to find greater fit to their optimality models in the behaviour of these human populations compared to post-industrialised societies. In comparison, evolutionary psychologists, whose research mainly focuses on Western populations, make no attempt to test whether psychological mechanisms, manifested through behaviour, are adaptive in modern human societies, as they are wedded to the adaptive lag hypothesis. In particular, the availability of contraception is often used as a means of dismissing any possible connection between how the mind works and actual reproductive success. Evolutionary psychologists even go so far as to argue that human behavioural ecologists are mis-directed in focusing their research on adaptive outcomes rather than on evolved psychological adaptations (SYMONS 1987). These disagreements have resulted in unresolved vigorous debates between evolutionary psychologists and human behavioural ecologists (DALY and WILSON 1999; 2000; SMITH et al. 2000; LALAND and BROWN 2002).

The concept of the environment of evolutionary adaptedness does provide a useful reminder that human behaviour has been influenced by selection pressures acting over the evolutionary history of our species, as for all other species. However, the adaptive-lag hypothesis assumes that few recent or current evolutionary pressures influence human cognition or behaviour. In contrast, the niche-construction perspective suggests that we should expect human behaviour to show a broad adaptive fit to the current environment, as niche-construction processes generally increase the short-term fitness of the constructor (ODLING-SMEE et al. 2003; LALAND and BROWN 2006). For instance, by adjusting their environments, organisms are able to regulate their environments in a way that can damp out selection pressures and preserve the adaptiveness of behaviour. As an example, the ability of our human ancestors to control temperature by manufacturing clothes and building shelters has dampened selection favouring anatomical and physiological responses to temperature extremes and fluctuations and allowed human beings to inhabit colder areas of the world. Just as in other species, such as termites who build nests in which air temperature is closely regulated, human niche construction activities are predicted to alter environments in a way that suits our previously-selected adaptations, resulting in little adaptive lag.

Where human niche construction activities do alter selection pressures, two possible responses may follow: genetic evolution and/or further niche-construction activities. An example of how cultural niche construction has induced a genetic response in humans is provided by a population of yam cultivators in West Africa, who cut clearings in forests to grow crops, with a cascade of consequences (DURHAM 1991). The clearings increased the amount of standing water, which provided breeding grounds for mosquitoes and increased the prevalence of malaria. This modified selection pressures in favour of an increase in the frequency of the hemoglobin *S* allele because, in the heterozygous condition, the *S* allele confers protection against malaria. As discussed earlier, analyses of the human genome have identified several genes that have undergone recent, rapid selection, including genes for malarial resistance (WANG et al. 2006; VOIGHT et al. 2006). Although genetic evolution is generally assumed to be slow, based on observed typical rates of response to selection (KINGSOLVER et al. 2001), significant genetic evolution can potentially occur in human beings over the course of a few hundred years, often in response to cultural niche construction activities (LALAND and BROWN 2006). In one sense this is a very different outcome to human cultural niche construction to the manufacturing clothes and building shelters example: here evolutionary change is precipitated rather than hindered. However, in another sense the outcome is the same – little adaptive lag. Here human modifications of the environment induce genetic change, resurrecting the fittedness of human genotypes to their constructed environment.

The second route by which human beings may respond to prior niche construction is through further niche construction. For example, suppose that human beings change their environment by polluting it. The problem may be alleviated subsequently by the invention and spread of a new technology that removes the contamination. Human populations exposed to the pollution may have experienced some adaptive lag while new technologies were being devised and adopted. However, their capacity of human beings to exhibit innovation, social learning and cumulative technology renders them particularly potent and rapid niche constructors. The ability to devise an adaptive cultural response to changes in the environment brought about by prior niche construction means that genetic evolution may not be the most common route by which human beings respond to environmental change. Cultural responses to modified selection pressures may occur more rapidly than genetic changes and may render genetic responses unnecessary (LALAND et al. 2001). Yet again, we would not predict extensive adaptive lag if human beings are able to respond to culturally-induced changes in the environment by further cultural niche construction (LALAND and BROWN 2006).

The assumption that human beings experience a large adaptive lag, such that human behaviour shows an adaptive fit to past, but not current, environments, is not supported by the niche-construction perspective. Niche construction activities will generally increase the fit between our modified environment and our previously-selected adaptations, partly because human beings respond to self-induced changes via further niche construction. While the psychological mechanisms of the human mind are often assumed to be too complex to change in response to rapid changes in selection pressures, as mentioned above, analyses of the human genome reveal strong evidence for recent selection on genes involved in neuronal function (WANG et al. 2006). Such apparently small changes could potentially bring about large changes in brain functioning. We recommend that the adaptive-lag hypothesis be rejected in favour of a niche-construction perspective, which focuses on how human beings respond, and are themselves responses, to self-induced environmental changes.

CONCLUSION

The recognition of niche construction as a cause of evolution has heuristic value within the human sciences. The emphasis of the niche-construction perspective on organisms in general, and humans in particular, as active constructors of their environment, and shapers of their own and other species' evolution, fits with the views of many human scientists and provides what ultimately will prove to be a more satisfactory evolutionary framework for understanding human behaviour.

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