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Niche Construction, Human Behavior, and the Adaptive-Lag Hypothesis

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Niche construction is the process whereby organisms modify selective environments, thereby affecting evolution. The niche-construction perspective is particularly relevant to researchers using evolutionary methods to interpret human behavior and society. On the basis of niche-construction theory, we argue against the hypothesis that modern humans experience an atypically large adaptive lag. We stress that humans construct their world largely to suit themselves and frequently buffer adaptive lag through cultural niche construction. Where they are unable to do that, natural selection of genes rapidly ensues. Our argument has implications for evolutionary psychology and human behavioral ecology, and suggests that the methods of the latter are potentially applicable to all human societies, even postindustrial ones.

Niche construction is the process whereby organisms, through their metabolism, activities, and choices, modify niches.[1] The niche-construction perspective was introduced to evolutionary biology in the 1980s,[2,3] but has been subject to increasing interest.[1,4–11] Advocates of the niche-construction standpoint seek to explain the adaptive complementarity of organism and environment in terms of a dynamic, reciprocal interaction between the processes of natural selection and niche construction.

Conversely, the conventional evolutionary perspective explains the organism-environment match solely in terms of natural selection. With many complications and caveats, such as frequency dependence and habitat selection, discussed by Odling-Smee, Laland, and Feldman,[1] adaptation is commonly seen as a process by which selection shapes organisms to fit preexisting environments. The causal arrow points in one direction only: Environments, as the source of selection, determine the features of living creatures. This directionality is captured by Williams[12]: "Adaptation is always asymmetrical; organisms adapt to their environment, never *vice versa*."

Yet organisms clearly change their environments. Numerous animals manufacture nests, burrows, holes, webs, and pupal cases; plants change levels of soil chemicals and modify nutrient cycles; fungi decompose organic matter; bacteria engage in decomposition and nutrient fixation (see Odling-Smee, Laland, and Feldman[1] for a review of this literature). Organisms also deplete and destroy important components of their world. Niche construction incorporates both positive and negative fitness ramifications of organisms' activities. Of course standard evolutionary theory does not deny niche construction, but interprets it as solely a product of evolution rather than as part of the process.

Organisms do not just build environmental components, but regulate them to damp out variability in environmental conditions. Beavers, earthworms, ants, and countless other animals build complex artifacts, regulate temperatures and humidities inside them, control nutrient cycling and stoichiometric ratios around them, and in the process construct and defend benign and apposite nursery environments for their offspring. Irrespective of the temperature outside the mound, termite larvae experience a relatively narrow and well-suited temperature range.[13] Termite nests are ideal for protecting the occupants

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from external extremes of temperatures, having a thick outer wall permeated with a labyrinth of fine galleries.[13] Experiments have shown that the internal temperature is appreciably damped relative to the external temperature.[14] Similar observations have been made with respect to birds' nests, and other animal structures.[13,15] From the niche-construction perspective, evolution is based on cycles of causation and feedback; organisms drive environmental change and organism-modified environments subsequently select organisms.[1–3,10] Nest building generates selection for nest elaboration, defense, and regulation.[1] Niche construction is not just an end product of evolution, but a cause of evolutionary change.

Standard evolutionary theory models the evolutionary consequences of niche construction solely in terms of fitness payoffs to the genes expressed in construction. For instance, the only widely considered feedback from a beaver's dam that is evolutionarily significant is that which affects the fitness of genes expressed in building this extended phenotype, relative to their alleles.[16] Niche-construction advocates regard this position as unsatisfactory. The standard approach ignores the importance of organisms' activities as a cause of evolution. When a beaver builds a dam, creating a lake and influencing river flow, this behavior not only affects the propagation of dam-building genes, but results in major changes in the local environment, affecting nutrient cycling, decomposition dynamics, the structure of the riparian zone, and plant and community composition and diversity.[17] It follows that dam building by beavers must alter the selection of other beaver traits, influencing beaver evolution. The active agency of beavers in modifying selection on themselves and other species currently goes unrecognized.

In recent years this feedback from organisms' activities has been subject to intense investigation through mathematical population-genetic analyses.[1,6,7] It is now well established that the selection modified by niche construction can be evolutionarily important, and can generate rich microevolutionary dynamics. By modifying selection, niche construction can create new evolutionary equilibria, affect the stability of other equilibria, generate momentum effects (populations continue to evolve after selection has stopped), and inertia effects (a delayed evolutionary response to selection), as well as opposite and catastrophic responses to selection.[1,6,7] In other words, the feedback that niche construction generates in evolution makes a difference to how organisms evolve.

This is also true for niche construction based on learning and cultural processes.[8] Acquired characters, such as learned behavior, exert their influence by modifying selection pressures. For instance, the Galapagos woodpecker finch learns asocially to use a cactus spine or similar implement to grub for insects in the bark of trees.[18] This behavior is not in any sense guaranteed by the presence of naturally selected genes, yet it has nonetheless modified the selection acting on these birds to favor a beak optimal for tool use rather than wood pecking.[1,18] The role of acquired characters becomes particularly significant for the evolution of vertebrates, as a result of their flexible, brain-based learning, and imprinting, song learning, social learning, and habitat imprinting, and various other forms of learning are now recognized as playing roles in evolution. The significance of acquired characters to evolutionary processes becomes further amplified with stable transgenerational culture. It is now widely believed that such characters were probably extremely important to hominid evolution.[19,20] The potency of human niche construction is immediately apparent. Our engineering and technology has tamed the planet, allowing us to exist in a fantastically broad range of habitats. Humans are equally at home foraging as hunter-gatherers on the African savanna, hunting fish and seals in the Arctic, or living in cities.

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To a large extent, it is our capacity for culture that makes us such effective niche constructors.[19,20] By culture, we mean the ability to acquire and transmit learned knowledge, beliefs, and skills and to devise ever more efficient solutions to problems that build on this reservoir of shared intelligence. Other animals possess traditions; for instance, there is chimpanzee tool use and chaffinch song dialects.[21] Yet human cultural processes are exceptionally potent compared to those in other animals, probably because of this cumulative property.

Recent mathematical population genetics theory demonstrates that niche construction does not have to be based on genes in order to affect the evolutionary process. Cultural niche construction, in which learned and socially transmitted behavior modifies environments, can also have major biological evolutionary consequences.[8,22,23] Indeed, theory suggests that culture amplifies the evolutionary feedback loop generated by niche construction.[1,8] Human evolution may be unique in that our culture and niche construction have become self-reinforcing, with transgenerational culture modifying the environment in a manner that favors ever more culture, and niche construction informed by cultural knowledge becoming ever more powerful.[24]

Box 1. The Co-evolution of Dairy Farming and Lactose Absorption

The argument that niche construction should be regarded as an evolutionary process is based on the observation that it can cause evolutionary events without itself being fully explained by any recognized evolutionary process. This is illustrated by the example of dairy farming. 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 is necessary to break down the lactose in dairy products. These differences relate to genetic variation.[58] A strong correlation exists across cultures between the presence of the genes for lactose absorption and a history of dairy farming.[71] This has led to the hypothesis that dairying created the selection pressures that led genes for lactose absorption to become common in pastoralist societies. Gene-culture coevolutionary analyses provide strong support for this hypothesis.[72,73] A comparative analysis by Holden and Mace[74] found that dairy farming spread before the genes for lactose absorption, not the other way around.

Dairy farming is an instance of human niche construction that is mediated by cultural processes. There are no genes for dairy farming. (We use "genes for" in the sense of Dawkins.[75]) Possessing genes for elevated lactase activity does not lead an individual to herd cattle and the presence of such genes cannot be used to predict who will keep cows. While the dairy farmer's genes are expressed when the cows are milked, these genes are not specialized to dairying; they are common to all human populations. Genes do not constitute the appropriate level of analysis to explain why individuals in some societies farm cattle and others do not. This is a cultural phenomenon and explanations at the genetic level would be overly reductionist. Moreover, dairy farming is not an adaptation (*sensu* Williams[76]), but rather an adaptive cultural practice. Yet in spite of the fact that dairy farming is not caused by genes and is not a product of natural selection, it has had clear evolutionary consequences. Many similar examples[1] support the argument that niche construction should be regarded as an evolutionary process in its own right.

NICHE CONSTRUCTION AND THE ADAPTIVENESS OF HUMAN BEHAVIOR

In the preceding section, we presented some of the reasons why advocates of the perspective view niche construction as a hitherto-unrecognized evolutionary process. Such advocates believe that niche construction should be regarded, alongside selection, drift, and mutation, as one of the primary causes of evolution. Endler[25] identified 21 such evolutionary "processes," including processes "that generate variation," "change frequencies of variants," and "affect the rate or direction of evolution." Although niche construction is absent from his list, it meets Endler's criteria for inclusion, most obviously as a factor that affects the direction of evolution. The case for treating niche construction as an evolutionary process is illustrated by examples such as the co-evolution of dairy farming and genes for lactose absorption (Box 1), a niche-constructing activity that has generated evolutionary change despite the fact that it is not caused by any recognized evolutionary process.

Naturally, the niche-construction perspective has evoked both positive and negative responses, and considerable debate among biologists.[9,26] It remains to be seen whether this perspective will become an established feature of evolutionary theory. While we believe the niche-construction framework will eventually prove of general utility, here we suggest that there are compelling reasons why it should be more overtly acceptable, less contentious, and of immediate utility to researchers studying human behavior. That is partly because of the clear potency of human niche construction. There can be no doubt that technology has massively changed environments. That fact, combined with the comparatively reduced role of genetic variation in causing human behavioral variation, means that human niche construction cannot be fully explained by prior natural selection.

There are already signs that evolutionarily minded human scientists, including philosophers, archeologists, anthropologists, psychologists, and primatologists, are starting to use niche construction. These include studies of antibiotic treatment and bacterial evolution,[23] small family size and the demographic transition,[22,27] primate social behavior,[28,29] cultural evolution,[30] biological anthropology,[31] cognitive evolution,[32,33] and extragenetic inheritance.[1,10,34] This work lends credence to the view that the niche-construction perspective will engender a progressive research program.

We have not space here to draw out the full implications of niche construction for the human sciences. Elsewhere, the reader can find discussion of the general implications of niche construction for human evolution and for evolutionary theories of human behavior, together with a variety of novel methods and hypotheses.[1] Here we focus specifically on the issue of adaptive lag and consider how a niche-construction perspective affects the standing of the research philosophies of two contemporary evolutionary approaches to the study of human behavior, namely human behavioral ecology and evolutionary psychology (see Laland and Brown[35] for a review of these and other evolutionary perspectives).

Human behavioral ecology emerged in the 1970s in the aftermath of the human sociobiology debate. As the name suggests, it consists of applying the methods of behavioral ecology to humans, treating them similarly to other animals (although also using information from interviews and written records). Human behavioral ecologists often explore the extent to which the behavioral differences observed between human groups are re sponses to particular environments.[36–38] Their aim is to determine how ecological and social factors affect behavioral variability within and between populations, and to predict patterns of behavior using mathematical models.

A key assumption of human behavioral ecology is that human beings are able to alter their behavior flexibly in response to environmental conditions in a manner that optimizes their lifetime reproductive success.[38] A second feature is the testing of hypotheses derived from mathematical models based on assumptions of optimality and fitness maximization, usually with data gathered on small communities in remote regions of the world. For example, Borgerhoff Mulder[39] studied the marriage practices in the Kipsigis to investigate whether the circumstances under which women will marry an already married man can be predicted with a polygyny threshold model that works well for animals. The model made effective predictions.

Human behavioral ecology has been subject to criticism from some evolutionary psychologists. For instance, Symons[40] argued that their research program was flawed because it did not formulate or test hypotheses concerning human adaptations or shed light on the human mind where such adaptations would be found. Other evolutionary psychologists joined in the attack, leading to a vigorous debate.[40–43] One alleged weakness of human behavioral ecology is that human behavior will not necessarily be adaptive in industrialized societies.[40,43–45] The argument is that modern environments, with their houses, cars, airplanes, shops, hospitals, guns, and computers, are extremely different from the environments in which the genus *Homo* evolved. Leading evolutionary psychologists to argue that over the last two million years our ancestors have spent most of their existence hunting and gathering in small groups in Africa.[43–45] They suggest that this history of selection will have fashioned human minds to be adapted to the ancestral world of the Pleistocene, the environment of evolutionary adaptedness, rather than its modern counterpart, arguing that human beings walk our modern streets with "stone-age brains in our heads."[44] "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" (Cosmides and Tooby,[45] p. 280–281).

Because evolution is a response to changed selection pressures, and that response cannot be instantaneous, it is a truism that all organisms must experience some adaptive lag, here meaning a mismatch between current selection pressures and behavior. In this respect, humans are not unique. However, leading evolutionary psychologists apparently believe that the adaptive lag for humans is atypically large, because human technology and innovation have changed human environments so extensively and so quickly. Henceforth, we shall refer to the idea that modern humans experience a large discordance in their selective environments compared to those to which they are adapted as the adaptive-lag hypothesis.

Based on insights gained from the niche-construction perspective, we put forward the counter proposal that niche-constructing activity generally increases the match between an animal's behavior and its environment.

Human behavioral ecologists typically respond to the putative problem of adaptive lag by stressing the flexibility of human behavior, which, they claim, allows humans to accommodate themselves to a wide range of circumstances.[42] They suggest that most aspects of human behavior are likely to depend in a facultative manner on the particular social and ecological resources to which they are exposed and that, because humans evolved as opportunistic ecological generalists in variable environments,[46] selection will have favored the ability to adopt the strategy that maximizes fitness in a given environment.[38]

Yet even the most adaptable of creatures will experience limits to its tolerance space, outside of which it is unable to behave adaptively. Could it be too much to expect humans to behave adaptively in modern industrialized worlds? The fact that human behavioral ecologists primarily study people living in preindustrial societies only reinforces the view that the adaptive-lag hypothesis may be correct, and that modern postindustrial societies may be too different from ancestral selective environments for humans to behave adaptively.

We believe the adaptive-lag hypothesis is misguided. Based on insights gained from the niche-construction perspective, we put forward the counter proposal that niche-constructing activity generally increases the match between an animal's behavior and its environment. We will describe three candidate reasons why human niche construction should typically be adaptive.

Reason 1: Humans Construct Their World to Suit Themselves

As they evolve, and even if they were to stop evolving genetically, humans continuously construct and reconstruct important components of their selective environments. In this respect, humans are no different from other organisms. Animals do not just perturb their environments at random, they build structures that are extended phenotypes, adaptations that enhance fitness.[16] Animals also deplete resources and pollute environments, but this too increases fitness in the short term and is often tied to life-history strategies that take account of this activity, for instance through dispersal or migration when resource levels are low or the environment becomes uninhabitable.[1] While niche construction can have both positive and negative effects on the constructor's fitness, Odling-Smee, Laland, and Feldman[1] are explicit about their expectation that most niche construction will increase the short-term fitness of the constructor, although it may have negative consequences for other species. This is hardly contentious: the fitness benefits of animal artifacts are well-documented.[13,15,16] Niche construction is typically functional and adaptive because it is informed, but not determined, by genes, and sometimes also by learning and culture.[1]

As described, animals do not just build structures, but regulate them to damp out variability in environmental conditions,[1] with the result that niche construction can maintain selection pressures and preserve the adaptiveness of behavior. Odling-Smee, Laland, and Feldman[1] define counteractive niche construction as occurring when organisms either perturb their environments or relocate in space to neutralize some prior change in selection pressures. While humans' ability to engage in counteractive niche construction is amplified by their capacity for culture, it is an extremely general phenomenon. Like the acorn-storing squirrel or the wasp that cools her nest with droplets of water, our ancestors ensured the availability of food by tracking game and storing food, and controlled temperature by manufacturing clothes and building fires and shelters. In principle, modern refrigerator-freezers and air conditioning are no different. Such niche construction may change environments, but it actually functions to negate a modified or fluctuating selection pressure, thereby reducing selection.[1] Human-built environments might be different from African savanna, but many selection pressures acting on us could be broadly similar, since our constructions were built to be suited to our bodies and their needs. (A related argument was put forward by Wilson.[47])

For illustration, imagine a population of our ancestors exposed to a fluctuating temperature, sometimes experiencing very hot conditions and sometimes cold. In the absence of niche construction, this would engender bouts of selection for genes expressed in hot and cold adaptations, and induce an adaptive lag. However, if humans can put on and take off clothes, build fires, find caves, and develop cooling systems, they negate these changed selection pressures. The temperatures actually experienced by the population are damped relative to the external environment and as a consequence there is little response to selection required and little adaptive lag. Now imagine that the environment becomes more arid and our ancestors respond by pumping or carrying in water for drinking and irrigation, or relocate to a less arid region. Again, they have negated selection that might otherwise have generated selection and adaptive lag. Counteractive niche construction acts to maintain environmental conditions within tolerable limits, and in the process filters and modifies the selection acting on the constructor.

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There are many real-life examples.[1] Selection favors physiological adaptation to an aquatic life in earthworms, in spite of the fact that these originally aquatic creatures long ago moved onto land.[48] This is possible only because earthworm niche construction (tunnelling, burrowing, casting, and such) modifies the soil environment to reduce soil matrix potentials, allowing the worms to draw large amounts of water into their bodies.[48] Their niche construction has conserved selection pressures, in spite of the massive change from aquatic to terrestrial environment.

Much of our constructed environment can be seen to be shaped to suit human bodies. A cup is a useful drinking utensil for a human, but of little utility to most other organisms, lacking, as they do, the manipulative dexterity of a limb with fine motor control within easy reach of a mouth. That is not because cup manufacturers are constrained by genes to design drinking implements with prespecified characteristics; it is because other designs have proved less useful. Cups, knives, forks, saucepans, ovens, kitchen cabinets, and countless other everyday tools, implements, and artifacts are specifically designed with human bodies in mind.

In spite of such design to our niche construction, its effect is not to produce a globally monotonous and constant environment: to the contrary. First, not all niche construction has this counteractive quality. Odling-Smee, Laland, and Feldman[1] also emphasize inceptive niche construction, where organisms perturb their environments or relocate to change a selection pressure, and stress its critical role in human evolution. Second, even counteractive niche construction only reduces environmental variability when considered on local scales. At larger scales, which include both engineered and nonengineered environments, there is evidence that niche-constructing activity increases diversity.[49] We are sympathetic to the view that environmental variability has selected for adaptability throughout human evolution,[50] but believe much of that variability was self-induced.

We could also emphasize the negative ramifications of human activities that occur through environmental degradation, resource depletion, and the resulting loss of biodiversity. There is little doubt that anthropogenic activities are driving other species extinct and this may have negative consequences for humanity in the longer term. Against this backdrop, our portrayal of human niche construction as positive and fitness enhancing may seem to gainsay the current consensus. In fact, this is not the case. We do not dispute that human niche construction has had devastating consequences for some other species, or that this activity may eventually have a negative impact on human fitness. Yet we reiterate our hypothesis that human niche construction typically has immediate fitness benefits to the constructor and to those who purchase constructed resources. Numbers of golden lion tamarins may dwindle, but in the meantime logging companies get rich, and many of us enjoy the security and comfort of wood-constructed homes and furniture. Indeed, the very success of human populations, with human fitness measured by intrinsic growth rates and resultant increases in population density, is a fundamental cause of overexploitation and habitat degradation.

Reason 2: Humans Frequently Buffer Adaptive Lag Through Cultural Niche Construction

Niche construction advocates note that organisms continuously choose or manufacture a suitable environment, often in response to environmental challenges created by their ancestors. Odling-Smee, Laland, and Feldman[1] collate extensive evidence, amounting to thousands of examples, of anatomical and behavioral traits that may be evolutionary responses to ancestral niche construction. These include elaborations of niche-constructed artifacts; physical or behavioral responses for regulating niche-constructed resources; courtship, mating, and parental behavior that evolved in response to prior niche construction; and multispecies co-evolutionary interactions mediated by niche construction.

Unlike most other species, humans can respond to ancestral niche construction in two ways:[1] through further (usually cultural) niche construction or through genetic evolution. The first means comprises an adaptive cultural response to a change in the environment that was brought about by earlier cultural niche construction. For example, suppose humans change their environment by polluting it. Subsequently, this polluted environment may stimulate the invention and spread of a new technology to cope with the contamination, alleviating the problem. If this happens, then the Route 1 loop would comprise a culturally induced change in an environment that favors the spread of a new technology. Provided the response is sufficiently effective to counteract the change in the environment, Route 1 should have no effect on human genetics and there will be no adaptive lag.

Consider the example of human aggregation into large sedentary communities, with the construction of towns and cities, which created, along with countless other challenges, the problem of what to do with human domestic and industrial waste products.[51] In such circumstances, human populations did temporarily experience novel self-induced selection pressures, very different from those witnessed by their African ancestors. For instance, they were exposed to a host of diseases, including measles, smallpox, and typhoid, that thrive in dense populations with poor sanitation.[51] At this juncture, then, there was an adaptive lag caused by cultural niche construction. Had these populations lacked the technology to respond to these challenges, either this adaptive lag would have been maintained, the population would have crashed, or genetic evolution would ensue. However, eventually, faced with disease and pollution, many human populations devised or adopted solutions, from sewerage plants to drains to water purification treatments that alleviated the problem.[51] Examples of this buffering of adaptive lag through cultural niche construction are commonplace: food shortages alleviated by new agricultural practices and innovations; water shortages eased by irrigation, pipelines, and reservoirs; extremes of climate by clothing, fires, and air-conditioning; and epidemics by vaccines and other medication.

Theoretical analyses suggest that cultural responses to modified selection pressures typically occur more rapidly than genetic responses do, and will often render genetic responses unnecessary. By rapidly responding to self-imposed problems through cultural niche construction, humans maintain their adaptiveness.

One consequence of the fact that cultural niche construction can damp out selection on human genes is that it can lead to increased numbers of genes in the human gene pool with potentially negative effects on fitness in the absence of these cultural activities. Such genes or genotypes are not appropriately characterized as being less adaptive than are alternatives, since adaptiveness is a property of phenotypes, although genes can obviously possess adaptive effects on the phenotype. The human phenotype includes any cultural influences on behavior that alleviate the diminishing effects on fitness conferred by such genetic characteristics. For instance, excessive reading and other close work by children has revealed genes that cause nearsightedness, genes that were not a problem in ancestral environments. However, the ability to manufacture prescription eyeglasses has once again relaxed the selection pressures on genes for myopia since, as long as we are wearing those glasses, our fitness is not greatly compromised.

While there is nothing inevitable about the capacity of human populations to construct solutions to self-imposed problems, their capacity for culture renders human niche construction uniquely potent and fast-acting, leaving Route 1 by far the more likely of the two responses to novel challenges. Other species also manifest constructed solutions to self-instigated problems, but these typically entail genetic evolution. For instance, by spinning webs spiders solve a foraging problem, but leave themselves vulnerable to predation from birds while on the web. Spiders of some genera overcome this by constructing dummy spiders out of silk and prey remains to deceive their predators, while others drag leaves, sticks, and other materials onto the web to hide behind, or mark the web to facilitate crypsis.[52] Such responses have evolved over long periods of time and involved large numbers of selective deaths among populations. While this, too, is a possibility for humans, as we will discuss next, theoretical analyses suggest that cultural responses to modified selection pressures typically occur more rapidly than genetic responses do, and will often render genetic responses unnecessary.[8] By rapidly responding to self-imposed problems through cultural niche construction, humans maintain their adaptiveness.

Reason 3: When Humans Are Unable to Buffer Adaptive Lag Fully Through Further Cultural Niche Construction, Natural Selection on Genes Ensues

Darwin emphasized the gradualistic character of evolution by natural selection, and for many years evolutionary biologists followed suit. More recently, biologists have been able to measure rates of response to selection in animals and plants, and the results suggest that selection may often operate faster than hitherto conceived. Indeed, selection experiments and observations of natural selection in the wild have led to the conclusion that biological evolution can be extremely fast, with significant genetic and phenotypic change sometimes observed in a handful of generations.[53–57] Recently, Kingsolver and colleagues[57] reviewed 63 studies that have measured the strength of natural selection in 62 species, including many vertebrates, with more than 2,500 estimates of rates of selection. They concluded that the median selection gradient was 0.16, which would cause a quantitative trait to change by one standard deviation in just 25 generations (c. 500 years for humans). This suggests that significant human evolution could be measured in hundreds of years or less.

This change in perspective on evolutionary rates opens the possibility that humans could realistically have evolved solutions to self-imposed problems over the last few millenia. This is illustrated by Route 2 and applies whenever human cultural processes fail to express a sufficiently effective response to an environmental change. In such cases, culturally modified environments give rise to modified natural selection pressures, which may change gene frequencies. For example, suppose there is no technology available to counter a new problem created by cultural niche construction, or suppose that the available technology is not exploited, possibly because it is too costly or because people are unaware of the impact of their activities on their environments. If such a situation persists for sufficient generations, then genotypes that are better suited to the culturally modified environment will increase in frequency, leading to evolutionary change.

For instance, there are several examples of culturally induced genetic responses to human agriculture.[1] One is provided by a population of Kwa-speaking yam cultivators in West Africa.[58] These people cut clearings in forests to grow crops, with a cascade of consequences. The clearings increased the amount of standing water, which provided better breeding grounds for mosquitoes and increased the prevalence of malaria. This, in turn, modified natural selection pressures in favor of an increase in the frequency of the sickle-cell *S* allele because, in the heterozygous condition, the *S* allele confers protection against malaria. Here culture has not damped out natural selection, but rather induced it. The fact that other Kwa-speakers, whose agricultural practices are different, do not show the same increase in the *S* allele frequency supports the conclusion that cultural practices can drive genetic evolution.[58]

Once again, this evolutionary change acts to restore adaptiveness. Among the malaria-rife regions of the Kwa homeland, being a heterozygote for the sickle-cell *S* allele is adaptive. Similarly, in dairying societies, genes expressed in high lactase activity pay fitness dividends. Malaria became a major health problem only after the invention of farming, a human cultural niche-constructing practice, yet there are several additional candidate genes that appear to have been favored by selection because they provide resistance to malaria. These include G6PD, TNFSF5, and alleles coding for hemoglobin C and Duffy blood groups.[59] There is also evidence that genes have been selected because they confer resistance to other modern diseases, including AIDS and smallpox (CCR5), and hypertension (AGT, CYP3A).[59] In all these cases, human modifications of the environment have only temporarily induced adaptive lag, this time alleviated through selection on genes.

Those evolutionary psychologists who emphasize human adaptive lag typically stress that human psychological mechanisms are complex adaptations based on co-adapted gene complexes that are unlikely to respond quickly to selection.[43–45] However, there are several problems with this argument. First, in virtually all cases the genetic bases of putative evolved psychological mechanisms are unknown. Second, there is currently little compelling evidence that human psychological mechanisms are complex adaptations. Indeed, many critics maintain that evolutionary psychologists have overestimated the degree of evolved structure in the mind.[35] Third, although comparatively little is known about the rates of evolutionary change of complex characters, the traits shown to respond quickly to selection are some elaborate, multi-loci ones.[57,60] Fourth, molecular genetic analyses reveal that small changes in genes, or in their promoters and enhancers, can bring about major changes in the functionality of complex characters.[61] Thus, at this juncture there is little neuroscientific or biological support for the evolutionary psychologists' argument.

IMPLICATIONS FOR THE STUDY OF HUMAN BEHAVIOR

How do we know that the three arguments presented earlier are correct and that human engineering, technology, and innovation are typically adaptive? One overwhelmingly compelling fact supports our assertion: human global population growth.[64] Ultimately, if human traits are largely adaptive, that will be manifest in high fitness, as exemplified by substantive intrinsic growth rates in human populations. Conversely, if contemporary human behavior is largely maladaptive, globally human numbers should dwindle. No such decline is expected for the foreseeable future.[62]

Herein lies a problem for advocates of the adaptive-lag hypothesis. It would be puzzling if our ancestors really started to thrive as soon as they left their environment of evolutionary adaptedness, yet it is in the Holocene, the period since the Pleistocene, that we see the explosion in human numbers and human colonization of the globe. This explosion is not attributable to expansion of hunter-gatherer societies. On the contrary, population growth appears linked to agricultural practices, technological advancement, medicine, and so forth, the phenomena that are most strikingly different from the Pleistocene environments of our ancestors. Growth in human populations provides the clearest indication that a major proportion of human characteristics remains adaptive even in modern constructed environments, which share hidden commonalities with those of our ancestors. Even postdemographic transition societies exhibit relatively stable population sizes or marginal growth or decline, indicative of largely adaptive behavior, rather than the substantial declines in numbers that should follow if behavioral practices were meaningfully maladaptive. There are now several theoretical articles proposing niche-construction hypotheses to explain this demographic transition.[22,27]

Evolutionary biologists recognize several different concepts of fitness; intrinsic growth rate is one of these.[60] However, intrinsic growth rate relates to absolute fitness, while most evolutionary biologists are concerned with the relative fitness of genotypes or traits. Nonetheless, comparisons between growth rates allow relative fitness to be estimated, and unless one wants to argue that nonagricultural practices in the Pleistocene conferred higher intrinsic growth rates than have modern practices in the Holocene, an assertion that we judge implausible, one is forced to the conclusion that these modern practices are not typically associated with a reduction in fitness, either relative or absolute.

Notwithstanding the preceding lines of reasoning, we do anticipate that human behavior will sometimes be maladaptive. Indeed, casual observations of cultural phenomena ranging from abstinent religious beliefs to destructive drug abuse, combined with the findings of population genetic theory, which reveals that maladaptive cultural traits can spread under a variety of circumstances,[19,20,37,63] convince us that there is nothing inevitable about adaptive human behavior. Richerson and Boyd[19,20] argue compellingly that selection cannot always eliminate the spread of maladaptive cultural variants because adaptive information is costly to evaluate, making the spread of some maladaptive traits an unavoidable byproduct of a generally adaptive cultural capability. Moreover, human beings are undoubtedly endowed with ancient evolved psychological adaptations that enable humans, for instance, to have complex family life, conform, fear strangers, and so forth.[19,20,64,65] However, we anticipate that it is the consistency of selection pressures over time, rather than the slow pace of selection, that best explains the existence of these legacies. Nonetheless, for the preceding reasons, we anticipate that adaptive human behavior will be the norm and maladaptiveness the exception. Furthermore, we see no reason to expect greater levels of adaptive behavior in preindustrial, small-scale, or hunter-gatherer societies than in the fully industrialized urban metropolis.

Population growth appears linked to agricultural practices, technological advancement, medicine, and so forth, the phenomena that are most strikingly different from the Pleistocene environments of our ancestors. Growth in human populations provides the clearest indication that a major proportion of human characteristics remains adaptive even in modern constructed environments.

Our three arguments describe events that are not instantaneous or unfailing, so naturally humans will still experience some adaptive lag. Our taste for salt, fat, and sugar provides a familiar example.[66] Plausibly valued as rare commodities by our ancestors, modern food production methods have solved the problem of scarce food for many of us, but we continue to crave these now-abundant foods to such an extent that we consume quantities that are excessive and sometimes lead to disease. Perhaps further cultural niche construction will eventually fix this problem through diet pills, medication, genetic engineering, or some such technology, or perhaps more tolerant genotypes will be favored by selection. Until then, however, an adaptive lag remains. Yet such examples are notable as exceptions. In spite of the massive changes humans have brought about in their worlds, we hypothesize that the aforementioned three factors collectively help to maintain a largely adaptive match between human features and the factors in their environments. We suspect that humans experience less adaptive lag than do comparable creatures such as other primates.

If correct, the niche-construction perspective provides a justification, based on evolutionary theory, for the widespread and general application of behavioral ecology methods to all human societies, including the most modern postindustrial societies. Substantive adaptive lags are likely to be sufficiently rare to render models that compute the optimal adaptive human behavior to be predictive most of the time. While we fully expect that there will be limited circumstances in which these methods are not effective, our point is that there is no good evolutionary reason to believe that the tools of behavioral ecology will not be successful in modern societies, in spite of the dramatic changes in our environments over the last few millennia. Furthermore, we argue that there is no valid evolutionary reason to expect the methods to be less successful in postindustrial than in preindustrial societies.

It might be argued that the use of behavioral ecological methods in modern societies is impractical, given the widespread use of contraception and the resulting disconnection between adaptive behavior and reproductive success. However, the strength of this argument is diminished on two counts. First, with notable exceptions,[67] any such disconnection is an unproven assumption, not an established fact. Second, even if reproductive success were to prove an ineffective currency, behavioral ecologists regularly exploit a range of different currencies, including various measures of foraging success, growth rates, and material wealth, many of which would still be of utility.

In summary, on evolutionary grounds we have argued against the hypothesis that modern humans experience an atypically large adaptive lag. We believe that the view that human minds are predominantly suited to an ancestral habitat portrays humans as passive products of past selection rather than as active constructors of their niches. Our arguments are all fairly intuitive, and we would be surprised if other researchers have not previously expressed similar views. In spite of this, the adaptive-lag hypothesis remains widely held, largely because it is regarded as supported by evolutionary theory. We hope that the alternative theoretical framework provided by niche construction will reinforce the counter-position and lend it greater authority. The niche-construction perspective is problematic for evolutionary psychology only to the extent that its research program is based on the assumption of adaptive lag. With regard to the apparently competing perspectives of human behavioral ecology and evolutionary psychology, we see strengths and weaknesses in both approaches, and have been advocates of pluralism within the field of evolution and human behavior.[37] Other evolutionary approaches to psychological phenomena, which place less emphasis on human adaptive lag, are entirely compatible with a niche-construction perspective.[20,68–70] Indeed, to the extent that the niche-construction viewpoint encourages evolutionary psychologists to consider that human behavior may currently be adaptive, it may further the rapprochement of human behavioral ecology and evolutionary psychology, and of these with other evolutionary perspectives on human behavior.

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