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Niche construction, biological evolution, and cultural change

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Abstract: We propose a conceptual model that maps the causal pathways relating biological evolution to cultural change. It builds on conventional evolutionary theory by placing emphasis on the capacity of organisms to modify sources of natural selection in their environment (niche construction) and by broadening the evolutionary dynamic to incorporate ontogenetic and cultural processes. In this model, phenotypes have a much more active role in evolution than generally conceived. This sheds light on hominid evolution, on the evolution of culture, and on altruism and cooperation. Culture amplifies the capacity of human beings to modify sources of natural selection in their environments to the point where that capacity raises some new questions about the processes of human adaptation.

Keywords: adaptation; altruism; cooperation; evolutionary psychology; gene-culture coevolution; human evolution; human genetics; niche construction; sociobiology

1. An evolutionary framework for the human sciences

The relationship between genetic evolution and culture raises two causal issues. The first concerns the extent to which contemporary human cultures are constrained or directed by our biological evolutionary heritage; the second concerns whether hominid genetic evolution has itself been influenced by cultural activities. We contend that these issues are inextricably tied: The significance of evolutionary theory to the human sciences cannot be fully appreciated without a more complete understanding of how phenotypes in general, and human beings in particular, modify significant sources of selection in their environments, thereby codirecting subsequent biological evolution. Our principal goal is to delineate and explore the interactions between biological evolution and cultural change.

Evolutionary biology has been widely invoked to account for human behaviour and social institutions. These explanations have generated sociobiology (Trivers 1985; Wilson 1975), human behavioural ecology (Borgerhoff Mulder 1991), and evolutionary psychology (Barkow et al. 1992), as well as evolutionism and social Darwinism (Kuper 1988). However, evolutionary approaches to human behaviour have provoked strong opposition, and the relevance of biological evolution to the human sciences remains widely disputed.

Less familiar, but equally deserving of attention, are empirical data and theoretical arguments suggesting that human cultural activities have influenced human genetic evolution by modifying sources of natural selection and altering genotype frequencies in some human populations (Bodmer & Cavalli-Sforza 1976; Durham 1991; Feldman & Laland 1996; Wilson 1985). Cultural traits, such as the use of tools, weapons, fire, cooking, symbols, language, and trade, may have also played important roles in driving hominid evolution in general and the evolution of the human brain in particular (Aiello & Wheeler 1995; Byrne & Whiten 1988; Dunbar 1993; Holloway 1981). It is likely that some cultural practices in contemporary human societies are still affecting human genetic evolution.

Historically, evolutionary theory has suggested only two possible routes via which feedback from human cultural activities could influence human genetic evolution. Human cultural activities may either directly change the genes that humans pass on to their descendants by generating mutations, or they may change the probability of humans surviving and reproducing. The first alternative was ruled out

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by the failure of Lamarkism. The so-called Weismann barrier effectively stops genes from being affected by any of the acquired characteristics of phenotypes, including the culturally acquired characteristics of human beings (Mayr 1982). Modern molecular biologists do interfere with genes directly on the basis of their acquired scientific experiences, but this innovation is too recent to have had any impact on human genetic evolution. The failure of this route therefore left only the second alternative, which encouraged sociobiology's claim that phenotypes of all species, including our own, reduce to "survival machines" or "vehicles" for their genes (Dawkins 1989) and that the only role phenotypes play in evolution is to survive and reproduce differentially in response to natural selection and chance. This subordinate status for phenotypes does not cut off human culture from human genetic evolution entirely, insofar as it still allows culture to contribute to human adaptations (Alexander 1979) and hence to genotypic fitnesses. However, according to this perspective, culture has no power to codirect human genetic evolution through active modification or creation of selection pressures.

Other evolutionary biologists maintain that culture frequently does affect the evolutionary process, and some have begun to develop mathematical and conceptual models of gene-culture coevolution that involve descriptions not only of how human genetic evolution influences culture but also of how human culture can drive or codirect at least some genetic changes in human populations (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981; Durham 1991; Feldman & Laland 1996). These models include culturally biased nonrandom mating systems (see, e.g., Aoki & Feldman 1997; Durham 1991; Laland 1994), the treatment of human sociocultural or linguistic environments as sources of natural selection (Aoki & Feldman 1987; Cavalli-Sforza & Feldman 1983), and the impact of different cultural activities on the transmission of certain diseases such as malaria and sickle-cell anaemia (Durham 1991). The common element among these cases is that cultural processes change the human selective environment and thereby affect which genotypes survive and reproduce.

Culture works on the basis of various kinds of transmission systems (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981), which collectively provide humans with a second, nongenetic "knowledge-carrying" inheritance system. If the cultural inheritance of an environment-modifying human activity persists for enough generations to generate a stable selection pressure, it will be able to codirect human genetic evolution. The culturally inherited traditions of pastoralism provide a case in point. Apparently, the persistent domestication of cattle, and the associated dairying activities, did alter the selective environments of some human populations for sufficient generations to select for genes that today confer greater adult lactose tolerance (Durham, 1991; Feldman & Cavalli-Sforza 1989).

This approach is explicitly species specific. Although other species of animals have their "protocultures" (Galef 1988), it has generally been assumed that *Homo sapiens* is the only extant species with cultural transmission stable enough to codirect genetic evolution (Boyd & Richerson 1985). If this is the case, "culture" can be used to explain little in primate evolution that happened prior to the appearance of powerful, accumulatory cultural inheritance.

We think this particular human-centred perspective is misleading. Humans may be unique in their extraordinary capacity for culture, but they are not unique in their capacity to modify natural selection pressures in their environments. Many other species do the same, either on the basis of simple protocultural traditions or, most often, without any help from culture at all (Jones et al. 1997; Lewontin 1983; Odling-Smee et al. 1996). We suggest that a deeper understanding of the relationship between genes and culture can be derived from evolutionary theory by demonstrating that humans are far from unique in their ability to change their own selective environments. Human culture may allow humans to modify and construct their niches, with spectacular ecological and evolutionary consequences, but niche construction is both general and pervasive and probably influences the ecology and evolution of many species.

1.1. Niche construction

Building on ideas initially developed by Lewontin (1983), we have previously proposed that biological evolution depends not only on natural selection and genetic inheritance but also on "niche construction" (Laland et al. 1996a; Odling-Smee 1988; Odling-Smee et al. 1996). *Niche construction* refers to the activities, choices, and metabolic processes of organisms, through which they define, choose,

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modify, and partly create their own niches.[1] It consists of the same processes that Jones et al. (1997) call "ecosystem engineering." For example, to varying degrees, organisms choose their own habitats, mates, and resources and construct important components of their local environments such as nests, holes, burrows, paths, webs, dams, and chemical environments. Many organisms also partly destroy their habitats, through stripping them of valuable resources or building up detritus, processes we refer to as *negative niche construction.*

Organisms may niche construct in ways that counteract natural selection, for example, by digging a burrow or migrating to avoid the cold, or they may niche construct in ways that introduce novel selection pressures, for example, by exploiting a new food resource, which might subsequently select for a new digestive enzyme. They might also do both, as when counteractive niche construction itself establishes a novel selection pressure by acting on a second trait, for example, when nest building is further elaborated to enhance defence. In every case, however, the niche construction modifies one or more sources of natural selection in a population's environment and, in so doing, generates a form of feedback in evolution that is not yet fully appreciated (Laland et al. 1996a; Lewontin 1983; Odling-Smee et al. 1996).

There are numerous examples of organisms choosing or changing their habitats, or of constructing artefacts, leading to an evolutionary response (Laland et al. 1996a; Odling-Smee et al. 1996). For example, spiders construct webs, leading to the subsequent evolution of various camouflage, protection, and communication behaviours on these webs (Edmunds 1974; Preston-Mafham & Preston-Mafham 1996). Similarly, ants, bees, wasps, and termites construct nests that often themselves become the source of selection for many nest regulatory, maintenance, and defence behaviour patterns. Many ant and termite species regulate temperature by plugging nest entrances at night or in the cold, by adjusting the height or shape of their mounds to optimise the intake of the sun's rays, or by carrying their brood around the nest to the place with the optimal temperature and humidity for their brood's development (Hansell 1984; von Frisch 1975). The construction of artefacts is equally common among vertebrates. Many mammals (including badgers, gophers, ground squirrels, hedgehogs, marmots, monotrema, moles, mole rats, opossums, prairie dogs, rabbits, and rats) construct burrow systems, some with underground passages, interconnected chambers, and multiple entrances (Nowak 1991). Here, too, there is evidence that burrow defence, maintenance, and regulation behaviours have evolved in response to selection pressures that were initiated by the construction of the burrow (Nowak 1991). In many of these examples there is strong comparative evidence suggesting that nest building is ancestral to the nest elaboration, defence, and regulatory behaviour (Hansell 1984; Nowak 1991; Preston-Mafham & Preston-Mafham 1996).

Most cases of niche construction, however, involve not the building of artefacts, but merely the selection or modification of habitats (Odling-Smee 1988). For example, many insects choose particular host plants as oviposition sites, greatly influencing the developmental (and hence selective) environment of the emerging larvae (see, e.g., Jaenike 1982). Nor is niche construction confined to animals. Plants, too, can change the chemical nature, the pattern of nutrient cycling, the temperature, humidity, fertility, acidity, and salinity of their soils (Ellis & Mellor 1995), and the patterns of light and shade in their habitats (Holmgren et al. 1997). For example, pine and chaparral species increase the likelihood of forest fires by accumulating oils or litter (Mount 1964). In this case a probable evolutionary consequence is that these species have evolved a resistance to fire, and some species require a fire before their seeds will germinate (Whelan 1995).

Niche-constructing organisms may also substantially modify the environment of their offspring, and even more distant descendants. Thus, generations of organisms inherit not only genes from their ancestors, but also a legacy of natural selection pressures that have been modified by ancestral niche construction. This legacy of modified selection pressures has previously been labelled an *ecological inheritance* by Odling-Smee (1988). Major differences between genetic inheritance and ecological inheritance include the fact that the former is transmitted internally from only one (asexual) or two (sexual) parents to offspring via reproduction, whereas the latter persists, or is actively maintained from one generation to the next, in the external environment by multiple organisms. Below we illustrate this legacy of modified selection pressures, by choosing a series of increasingly complicated examples, starting with the simplest case, in which the effects of niche construction are confined to a single generation.

All organisms constantly interact with their local environments, and they constantly change them by doing so. If, in each generation, populations of organisms modify their local environment only idiosyncratically or inconsistently, then there will be no modification of natural selection pressures and, hence, no significant evolutionary consequence. If, however, in each generation, each organism repeatedly changes its own environment in the same way, perhaps because each individual inherits the same genes causing it to do so, then the result may be a modification of natural selection. The environmental consequences of such niche construction may be transitory, and may still be restricted to single generations, but if the same environmental change is reimposed for sufficient generations, it can serve as a significant source of selection.

Web spiders provide an example. Individual spiders repeatedly build webs in their local environments, generation after generation, presumably because they repeatedly inherit genes expressed in web construction. The consistent presence of a web in each spider's environment has, over many generations, fed back to become the source of new natural selection pressures for further phenotypic changes in the population of spiders, such as the marking of the web to enhance crypsis, differential responses to the frequency of web vibration, or the building of dummy spiders in their webs by *Cyclosa* to divert the attention of bird predators away from themselves (Preston-Mafham & Preston-Mafham 1996). Although this feedback from niche construction influences the natural selection of genes from one generation to the next, it does not introduce an ecological inheritance to evolution, because no consequence of niche construction affects the next generation via the external environment.

In more complicated cases, inherited genes may be expressed in a modification of the environments of offspring, rather than in organisms' own environments. Here, the consequences of niche construction are effectively trans-

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mitted from one generation to the next via an external environment, in the form of parentally modified natural selection pressures. This transmission is sufficient to establish an ecological inheritance. For example, cuckoo parents repeatedly select host nests for their offspring, thereby bequeathing modified selection pressures, as well as genes, to their chicks. These modified selection pressures have probably favoured adaptations in the offspring of cuckoos, such as their short incubation periods or the behavioural ejection by cuckoo chicks of host eggs from the parasitized nests (Krebs & Davies 1993). Parents in vast numbers of species, across broad taxa, act in ways that influence the developmental environments of their offspring, for example, by providing them with benign nest environments or with food. This kind of extragenetic inheritance, between two succeeding generations, is now widely recognised and can be modelled as a "maternal" inheritance (Feldman & Cavalli-Sforza 1976; Kirkpatrick & Lande 1989; West et al. 1988; Wolf et al. 1998).

Maternal inheritance, however, is itself only a restricted case of a more general phenomenon, because the effects of niche construction readily generalise from two generations to multiple generations, and from mothers only to multiple ancestors of both sexes. For example, through their burrowing activities, their dragging of organic material into the soil, their mixing of organic material with inorganic material, and their casting (which serves as the basis for microbial activity), earthworms dramatically change both the structure and the chemistry of soils (Darwin 1881; Lee 1985). As a result, contemporary earthworms live in worlds that have been partly niche-constructed by many generations of ancestors. Other earthworm phenotypes, such as epidermis structure or the amount of mucus secreted, have probably coevolved with such niche-constructing behaviour.

Figure 1 shows how niche construction and ecological inheritance interact with natural selection and genetic inheritance. Figure 1a represents the standard evolutionary perspective: Populations of organisms transmit genes from one generation to the next, under the direction of natural selection. Figure 1b extends this perspective to acknowledge that phenotypes modify their local environments through niche construction. Genes are transmitted by ancestral organisms to their descendants, exactly as the standard theory describes, but, in addition, phenotypically selected habitats, phenotypically modified habitats, and artefacts persist, or are actively or effectively "transmitted" by the same organisms to their descendants via their local environments. The environments encountered by descendent organisms are not just "templates" to which organisms adapt. Environments are partly determined by independent environmental events (for example, climatic, geological, or chemical events), but also partly by ancestral niche construction.

The evolutionary significance of niche construction hangs primarily on the feedback it generates. Many organisms modify their own selection pressures, so that environment-altering traits coevolve with traits whose fitness depends on alterable sources of natural selection in environments. Such feedback cycles may be indirect, so that they operate via a series of other environmental components, which may be biotic, such as other coevolving populations, or abiotic, such as soil chemistry or a water resource (Odling-Smee et al. 1996). These indirect routes can become complicated, and may even incorporate entire biogeochemical cycles in ecosystems.

The changes that organisms cause in their niches, and the resulting dynamics, are seldom investigated in empirical evolutionary studies or incorporated into population ge-

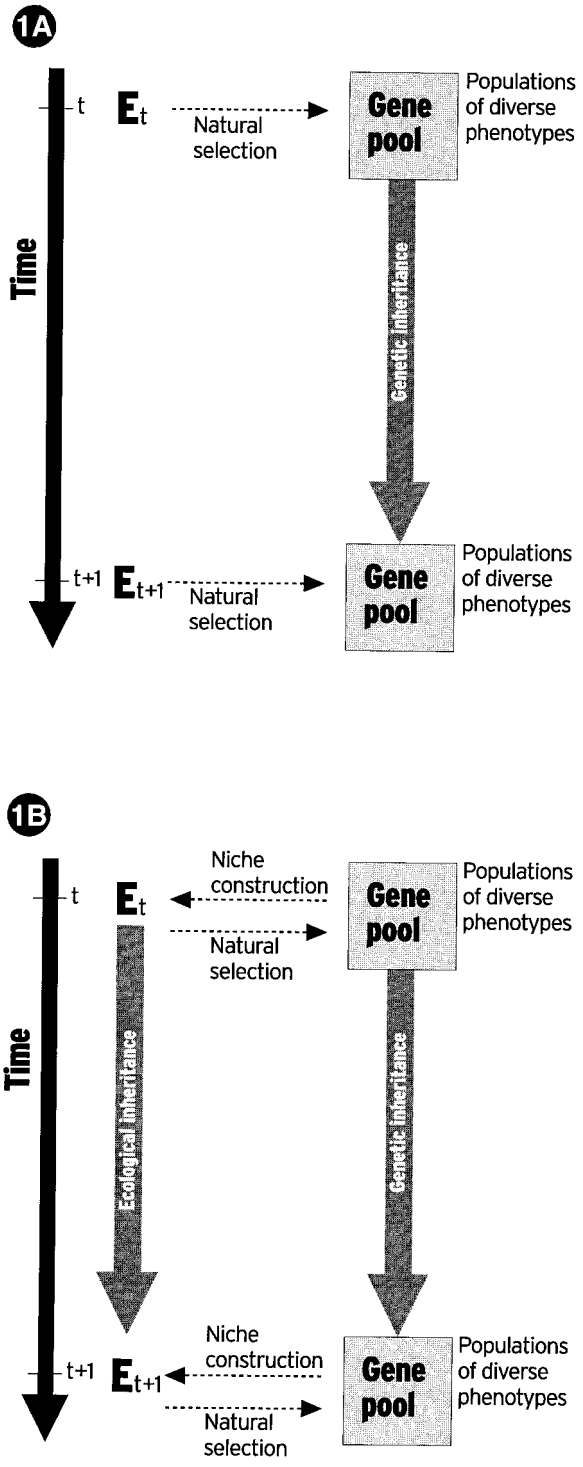


Figure 1. (a) Standard evolutionary perspective: Populations of organisms transmit genes from one generation to the next, under the direction of natural selection. (b) With niche construction: Phenotypes modify their local environments (E) through niche construction. Each generation inherits both genes and a legacy of modified selection pressures (ecological inheritance) from ancestral organisms.

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netic models. One theoretical construct that captures some, but not all, of the consequences of niche construction is Dawkins's (1982) "extended phenotype." Dawkins argues that genes can express themselves outside the bodies of the organisms that carry them. For example, the beaver's dam is an extended phenotypic effect of beaver genes. Like any other aspect of the phenotype, extended phenotypes play an evolutionary role by influencing the chances that the genes responsible for the extended phenotypic trait will be passed on to the next generation. Dawkins emphasises this single aspect of the evolutionary feedback from niche construction. However, the beaver's dam sets up a host of selection pressures, which feed back to act not only on the genes responsible for the extended phenotype, but also on other genes that may influence the expression of other traits in beavers, such as the teeth, tail, feeding behaviour, susceptibility to predation or disease, social system, and many other aspects of their phenotypes. It may also affect many future generations of beavers that may "inherit" the dam, its lodge, and the altered river or stream, as well as many other species of organisms that now have to live in a world with a lake in it.

Other topics in population biology are concerned with the evolutionary consequences of the changes that organisms bring about in their own and in other populations' selective environments. For example, habitat selection, frequency- and density-dependent selection, and coevolution involve phenotypic effects that may feed back to affect fitness (Maynard-Smith 1989). So far, however, most analyses of these subjects have focused only on those loci that influence the production of the niche-constructing phenotype itself. What is missing is an exploration of the feedback effects on other loci, exploring how traits that alter selection pressures coevolve with other traits favoured by these changed selection pressures.

We have begun the development of a body of theory that sets out to explore the evolutionary consequences of niche construction in a systematic manner (Laland et al. 1996a; 1999). Our theoretical analyses, which employed two-locus, population-genetic models, uncovered a number of interesting evolutionary consequences of the feedback from niche construction. We found that the selection resulting from niche construction sometimes overrides independent sources of selection, driving populations along alternative evolutionary trajectories, and may even initiate new evolutionary episodes in an unchanging external environment. Niche construction may influence the amount of genetic variation in a population by affecting the stability of polymorphic equilibria. Moreover, because of the multigenerational properties of ecological inheritance, niche construction can generate unusual evolutionary dynamics. For example, time-lags were found between the onset of a new niche-constructing behaviour and the response of a population to a selection pressure modified by this niche construction. These time-lags generated an evolutionary inertia, where unusually strong selection is required to move a population away from an equilibrium and a momentum, where populations continue to evolve in a particular direction, even if selection pressures change or are reversed.

Although these findings are novel, they are consistent with those of related theoretical analyses. For example, Robertson (1991) concluded that, because adapted organisms are both consequences of, and sources of, natural selection, both positive and negative feedback loops should be pervasive in evolution. These feedback loops introduce major instabilities, associated primarily with positive feedback cycles, and hyperstabilities, associated with negative feedback cycles. Feedback can produce "lock-in" effects, in which very small initial differences between alternative adaptations in species can be powerfully amplified by positive feedback loops resulting from a frequency-dependent fitness advantage to the most common variant. This variant may then rapidly become dominant, driving all competitors to become extinct. Theoretical analyses of maternal inheritance also report unusual evolutionary dynamics, such as time-lags in the response to selection, and evolutionary momentum (Feldman & Cavalli-Sforza 1976; Kirkpatrick & Lande 1989).

This small but growing body of theory suggests that niche construction and ecological inheritance may be of greater evolutionary importance than generally conceived. In our view, the capacity of populations of organisms to modify their selective environment through niche construction, and the fact that many of these changes persist for multiple generations, demand an adjustment in our understanding of the evolutionary dynamic, because they suggest that a description of evolutionary change relative only to independent environments is rather restrictive. In the presence of niche construction, adaptation ceases to be a one-way process, exclusively a response to environmentally imposed problems; it becomes instead a two-way process, with populations of organisms setting as well as solving problems. (Lewontin 1983; Odling-Smee et al. 1996). Evolution consists of mutual and simultaneous processes of natural selection and niche construction.

We have outlined the principal evolutionary consequences of niche construction elsewhere (Laland et al. 1996a; 1999; Odling-Smee et al. 1996). Our goal here is to spell out the repercussions of this perspective for the human social sciences. We maintain that a focus on niche construction has important implications for the relationship between genetic evolution and cultural processes. The replacement of a single role for phenotypes in evolution by a dual role immediately takes away from human culture its claim to a unique status with respect to its capacity to modify natural selection. Humans can and do modify many natural selection pressures in their environments, but the same may be said of many species, and most do so without the help of culture. Moreover, this dual role for phenotypes implies that a complete understanding of the relationship between genes and culture must not only acknowledge genetic and cultural inheritance, but also the legacy of modified selection pressures in environments. To illustrate these points, we must take a fresh look at how human culture relates to human evolution in the light of niche construction.

1.2. Relationship between evolution and culture

There is considerable disagreement over the relationship between evolution and culture. In Figure 2, we set out to elucidate how three independent approaches – human sociobiology, contemporary gene-culture coevolutionary theory, and our own proposed extension of gene-culture coevolutionary theory – model these interactions.

1.2.1. Human sociobiology. The conceptual model in Figure 2a represents the perspective of much human sociobi-

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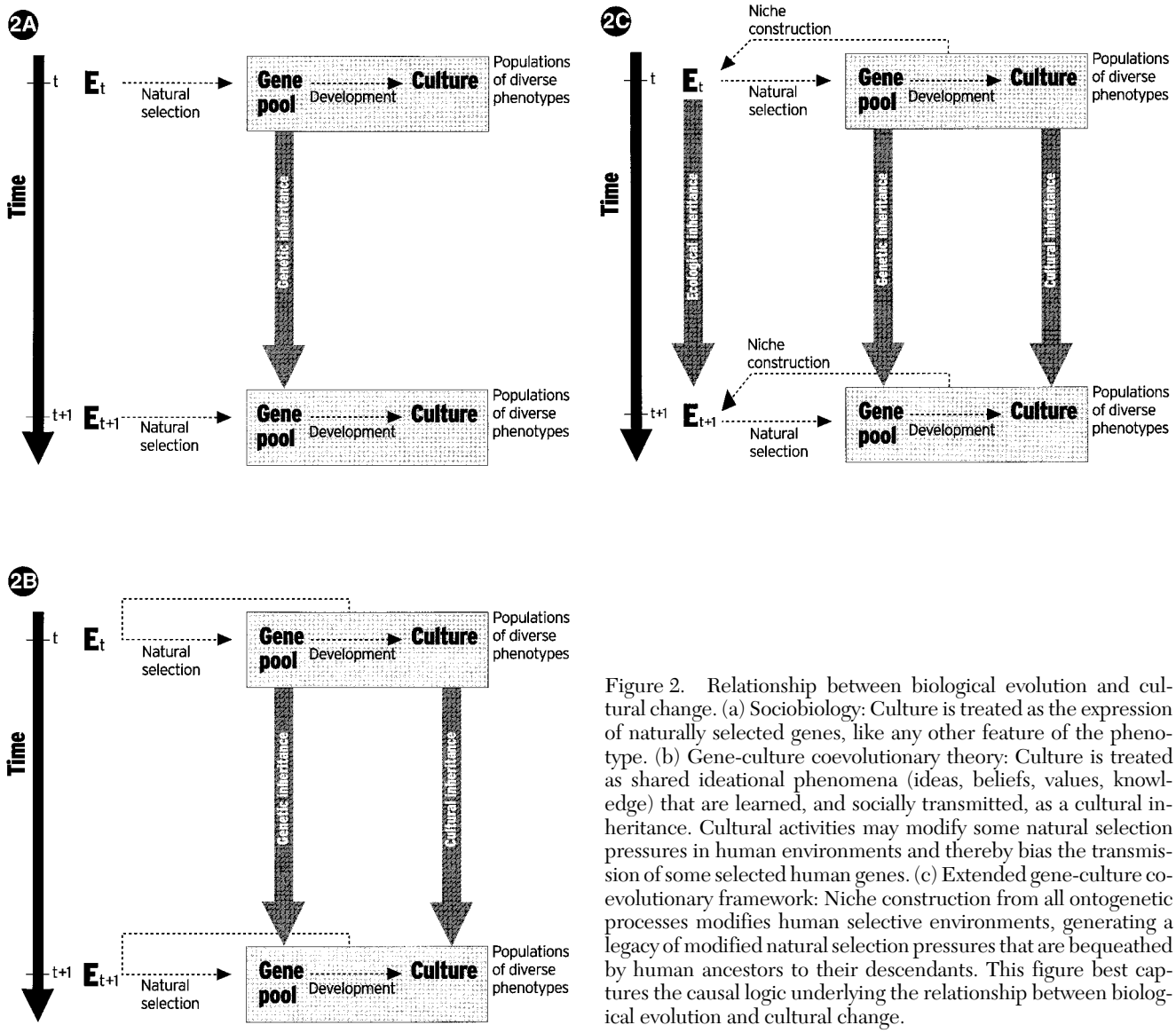


Figure 2. Relationship between biological evolution and cultural change. (a) Sociobiology: Culture is treated as the expression of naturally selected genes, like any other feature of the phenotype. (b) Gene-culture coevolutionary theory: Culture is treated as shared ideational phenomena (ideas, beliefs, values, knowledge) that are learned, and socially transmitted, as a cultural inheritance. Cultural activities may modify some natural selection pressures in human environments and thereby bias the transmission of some selected human genes. (c) Extended gene-culture coevolutionary framework: Niche construction from all ontogenetic processes modifies human selective environments, generating a legacy of modified natural selection pressures that are bequeathed by human ancestors to their descendants. This figure best captures the causal logic underlying the relationship between biological evolution and cultural change.

ology (Alexander 1979; Trivers 1985; Wilson 1975) and is built on the standard evolutionary viewpoint portrayed in Figure 1a. Here the potential interactions between biological evolution and cultural change are extremely simple. "Culture" is treated as the expression of naturally selected genes, like any other feature of the phenotype. From the sociobiological standpoint, the only way development and culture can affect genetic evolution is by influencing the adaptations of individual organisms and, hence, the probability that different individuals in a population will survive and reproduce to pass on their genes to the next generation. However, this initial conceptual model is too restricted and leaves us with a rather poor understanding of how human genetic evolution interacts with human cultural life. For example, the sociobiological perspective largely neglects cultural inheritance and ignores the fact that cultural activities can modify selection pressures in human environments (Bodmer & Cavalli-Sforza 1976; Durham 1991; Feldman & Laland 1996).

The scheme portrayed in Figure 2a has also fostered the equally simple contrary view, maintained by many of the critics of sociobiology (Montagu 1980; Sahlins 1976) that, at least in modern humans, cultural inheritance is so powerful that in many cases it no longer interacts with genetic inheritance at all but overrules it. This position fails to explain many relevant data that indicate that, to varying degrees, human cultural processes are constrained by human genes, and could not work unless they were because they need a priori knowledge in the form of evolved, genetically encoded information to get started (Barkow et al. 1992; Daly & Wilson 1983; Durham 1991). For example, there is now considerable evidence that evolved linguistic predispositions, as well as other generative capacities, exist in human brains, and are presumably subject to developmental processes that are constrained by genes (Barkow et al. 1992; Pinker 1994). Therefore, culture cannot always be meaningfully decoupled from genetics. It is important to recognize, however, that genetic influences on human behaviour are rarely straightforward, and that these influences may dissipate or become obscure when human relationships and social institutions are brought into focus (Hinde 1987).

1.2.2. Gene-culture coevolution. Dissatisfaction with both sociobiology, and the critics of sociobiology, eventually led

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to the development of gene-culture coevolutionary theory[2] (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981; Durham 1991), portrayed in Figure 2b. Gene-culture coevolution is still based on standard evolutionary theory (Figure 1a), except that here the interactions between human genetic evolution and culture become richer. Culture is treated as shared information (ideas, beliefs, values) that is learned, expressed in cultural activities, and socially transmitted between individuals in the form of a cultural inheritance. This concept of culture is deliberately restricted, abandoning more diffuse and all-encompassing notions of culture common in the human sciences (e.g., Tylor 1871), while building on ideational perspectives, in an attempt to operationalize the units of cultural transmission (Durham 1991). The novelty of the gene-culture approach is that it assumes that some human cultural activities may feed back to modify some selection pressures in human environments, so cultural transmission may affect the fate of some selected human genes. Thus, in Figure 2b, the relevant aspect of human selective environments is defined as cultural. This selection arises from the impact of cultural activities on human environments and is sufficient to allow humans some power to codirect their own evolution.

The conceptual model presented in Figure 2b extends Figure 2a, yet it still oversimplifies the causal pathways connecting genes and culture, because it requires cultural inheritance to affect the fate of some human genes directly, in the absence of any other mediating process. In most cases where gene-culture coevolutionary theory has been applied, this assumption is reasonable. Culture may bias human mating patterns nonrandomly; it may bias other human interactions, such as trade or warfare, or it may bias the choice of which infants are selected for infanticide (Boyd & Richerson 1985; Kumm et al. 1994; Laland 1994). The assumption that human cultural inheritance can directly bias human genetic inheritance may also be acceptable even when the source of the natural selection pressure that is modified by culture is no longer human, provided the relationship between whatever cultural trait is being expressed and whatever natural selection pressure it is modifying is sufficiently direct. For example, the trait that affected human genetic evolution in the lactose-tolerance case was milk usage (Durham 1991). Here, gene-culture theory is again applicable, because the link between milk usage and its genetic consequences is sufficiently simple to allow it to be modelled without bringing in any intermediate variables (Feldman & Cavalli-Sforza 1989) .

1.2.3. Gene-culture coevolution plus niche construction. The gene-culture coevolutionary approach fails in more complicated situations, however. Take, for example, the case of Kwa-speaking yam cultivators in West Africa, who increased the frequency of a gene for sickle-cell anaemia in their own population as a result of the indirect effects of yam cultivation. These people traditionally cut clearings in the rainforest, creating more standing water and increasing the breeding grounds for malaria-carrying mosquitoes. This, in turn, intensifies selection for the sickle-cell allele because of the protection offered by this allele against malaria in the heterozygotic condition (Durham 1991). Here the causal chain is so long that simply plotting the cultural trait of yam cultivation against the frequency of the sickle-cell allele would be insufficient to yield a clear relationship between the cultural trait and allele frequencies (Durham 1991). The crucial variable is probably the amount of standing water in the environment caused by the yam cultivation, but standing water is an ecological variable, not a cultural variable, and it partly depends on factors (e.g., rainfall) that are beyond the control of the population. Thus, here, the simplifying assumption of a direct link between cultural inheritance and genetic inheritance distorts reality too much to allow their interaction to be modelled in the standard way. This time the two human inheritance systems can interact only via an intermediate, abiotic, ecological variable, which should be included to complete the model.

This shortcoming leads us to propose an extended gene-culture coevolutionary theory, a conceptual version of which is shown in Figure 2c. The novelty here is the replacement of the genetic inheritance scheme, described in standard evolutionary theory (Fig. 1a), as the proper basis of gene-culture coevolution, by the extended evolutionary scheme incorporating niche construction, summarised in Figure 1b. Thus in Figure 2c, niche construction from all ontogenetic and cultural processes modifies human selective environments. Culturally modified selection pressures are now regarded not as unique, but simply as part of a more general legacy of modified natural selection pressures bequeathed by human ancestors to their descendants. Hence, instead of being exclusively responsible for allowing us to codirect our own evolution, in contrast to what happens in every other species, culture now becomes merely the principal way in which we humans do the same thing that most other species do.

1.3. Multiple processes in evolution

We now take a closer look at the set of processes by which populations of complex organisms, such as humans, acquire adaptive information, and how this information is expressed in niche construction. It is now widely recognised that several of the major evolutionary transitions involved changes in the way information is acquired, stored, and transmitted (Szathmary & Maynard-Smith 1995). This is reflected in Figure 3, where we acknowledge that populations of complex organisms can acquire relevant semantic "information," or, more accurately, "knowledge" (Holland 1992) through a set of information-acquiring processes (Holland 1992) operating at three different levels, and with the knowledge gained being influenced by niche-constructed environments at each level. In various combinations, these are the processes that supply all organisms with the knowledge that organises their adaptations. Every species is informed by naturally selected genes, and many are also informed by complex, information-acquiring ontogenetic processes, such as learning or the immune system, whereas hominids, and perhaps a few other species, are also informed by culture. It is generally recognised that any comprehensive treatment of the gene-culture relationship requires the inclusion of all three sets of processes because the links between genetic evolution and culture cannot be understood without some reference to the intermediate ontogenetic processes, such as individual learning, that connect them (Boyd & Richerson 1985; Durham 1991; Feldman & Laland 1996; Plotkin & Odling-Smee 1981).

The most phylogenetically ancient process ultimately responsible for niche construction is genetic evolution. As a consequence of the differential survival and reproduction

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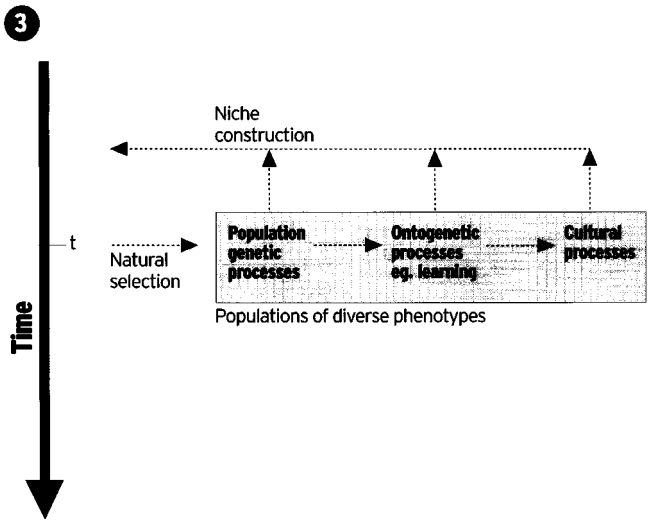


Figure 3. This figure zooms in on one of the boxes labelled "Populations of phenotypes" in Figure 2. Human evolution results from information-acquiring processes at three levels. Adaptation in populations of complex organisms, such as humans, depends on population genetic processes, information-acquiring ontogenetic processes, and cultural processes, all of which can generate niche construction.

of individuals with distinct genotypes, genetic evolution results in the acquisition, inheritance, and transmission of genetically encoded "knowledge" by individuals in populations. Each individual inherits this genetic information from its ancestors and then translates it into developmental processes, expressing different phenotypes in different environments, the so-called norm of reaction. Each individual may also contribute to the modification of its population's selective environment by genetically guided niche construction.

Many species have also evolved a set of more complicated ontogenetic processes that allow individual organisms to acquire another kind of information. These processes are themselves products of genetic evolution but are nevertheless distinct from it. They comprise "facultative" or "open" developmental processes, based on specialised information-acquiring subsystems in individual organisms, such as the immune system in vertebrates or brain-based learning in animals, and they are capable of additional, individually based, information acquisition. Here, the information-acquiring entity is no longer an evolving population, but is instead each individual organism in a population. As a result, the adaptive knowledge acquired through these ontogenetic processes cannot be inherited, because all the knowledge gained by individuals during their lives is erased when they die. Nonetheless, processes such as learning can still be of considerable importance to subsequent generations, because learned knowledge can guide niche construction.

A few species, including many vertebrates, have also evolved a capacity to learn from other individuals, and to transmit some of their own learned knowledge to others. In humans this ability is facilitated by additional processes (e.g., language), which collectively underlie culture. Culture adds a second knowledge-inheritance system to the evolutionary process through which socially learned information is accrued, stored, and transmitted between individuals. Here, the information-acquiring entity is again a group of interacting organisms rather than an individual. Although all cultural knowledge is traceable to the innovation and learning by particular individuals (with ontogenetic processes the ultimate source), major cultural changes may also occur through learning from neighbouring groups or immigrants, and may come with a baggage of associated ideological or organisational requirements.

Within a population, individuals share at least some of their learned knowledge with others, within and between generations. This information sharing can depend on several kinds of cultural inheritance, including vertical (from parents), horizontal (from peers), oblique (from unrelated older individuals), indirect (e.g., from key individuals), and frequency-dependent (e.g. from the majority) cultural transmission systems (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981). Cultural inheritance therefore requires at least one nongenetic channel of communication among organisms via which learned knowledge can be shared and spread. It probably also requires organisms to be able to decompose their store of cultural "knowledge" into discrete, transmittable "chunks" (Feldman & Cavalli-Sforza 1976), or "memes" (Dawkins 1989), perhaps equivalent to the psychologist's "schemata," in either simple or compound form (Holland et al. 1986; Plotkin 1996). In practice, in every species that is capable of sharing learned information, cultural inheritance depends on some kind of social learning (Durham 1991; Galef 1988); in humans, it may also depend on language (Pinker 1994).

Much of human niche construction is dominated by socially learned knowledge and cultural inheritance, but the transmission and acquisition of this knowledge are themselves dependent on preexisting information acquired through genetic evolution or complex ontogenetic processes. Thus, whereas the variants that occur during genetic evolution (i.e., mutations) are random (or at least blind relative to natural selection), those acquired through ontogenetic processes are not. As well as being selected by ontogenetic processes, any knowledge gain by individuals is guided by genetic information. For example, animals are genetically predisposed to respond to both specific internal cues (e.g., hunger) and environmental contexts (e.g., sensory cues indicating that food is nearby) by generating appropriate behaviour patterns from their repertoires. Hence, during learning, animals typically demonstrate a priori biases in their associations and patterns of behaviour that are most likely to be adaptive (Bolles 1970; Seligman 1970). In addition, those associations and patterns of behaviour that animals do learn critically depend on which stimuli are perceived as reinforcing (pleasant or painful) under the influence of species-specific motivational systems, and these perceptual and motivational processes are constrained by genes (Hinde & Stevenson Hinde 1973; Plotkin & Odling-Smee 1981). This means that the behaviours of an animal, the associations it forms, the antibodies it generates, the developmental pathways it takes, are typically, although not universally, functional and adaptive. By the same reasoning, as well as being selected by cultural processes, cultural knowledge is guided and constrained by both genetic information and by ontogenetic processes (Odling-Smee 1994). Social learning and transmission are affected by individual reinforcement histories and past associations partly because the cultural selective processes

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are themselves guided by what Durham (1991) calls *primary* (or *developmental*) *values*, as well as by socially transmitted cultural values. Therefore, with some caveats that we discuss in the final section, we expect that the ideas, values, and acquired knowledge that make up a culture would usually be adaptive.

We have now come some way from the simple, sociobiological descriptions of gene-culture interactions, captured in Figure 2a. We have brought together two different bodies of theory, gene-culture coevolution and niche construction. As a result, there is a proliferation of interactions between niche-constructing processes, biological evolution, and culture, as shown in Figure 2c. This proliferation is summarised in Table 1, which illustrates each interaction with an example, organised in terms of the sources and consequences of niche construction.

We believe that due recognition of the role of niche construction in the evolutionary dynamic should advance our understanding of the relationship between human culture and human genetic evolution. As such, our perspective may be regarded as part of a movement working towards a framework for integrating biology and the behavioural sciences (Durham 1991; Hinde 1987).

2. Illustrating the framework

What happens to those evolutionary and cultural issues that concern the human sciences when our new framework is substituted for the standard evolutionary perspective? In this section we will start to answer this question by describing some examples of how the feedback that occurs in our extended version of gene-culture coevolution might work. The examples we have chosen are hominid evolution, altruism and cooperation, and the processes of human adaptation.

2.1. Example 1: Hominid evolution

Archeologists and anthropologists currently seek to reconstruct the evolutionary history of modern humans from fossil and molecular data, in the context of standard evolutionary theory (Fig. 1a). Because this theory does not incorporate niche construction, it encourages the idea that human evolution must have been directed solely by independent natural selection pressures in human selective environments – that is, by selection pressures that have not been modified by niche construction. These selection pressures may sometimes include those arising from hominid social interactions (see, e.g., Byrne & Whiten 1988; Dunbar 1993; Durham1991; Foley 1996), but they do not include other sources of selection in the external environment that have been modified by ancestral hominid niche constructors. When human adaptation is treated as dependent not only on natural selection but also on niche construction (Fig. 2c), the suite of hypotheses about the causes, rates, and processes of evolutionary change is considerably enlarged.

2.1.1. Processes of human evolution. Consider the possible ways in which a new evolutionary episode might be initiated in hominid evolution. For illustrative purposes only, we consider a suite of explanations for the divergence of the lineages leading to the Pongidae and Hominidae families in the late Miocene, and we assume two ancestral populations in allopatry. The subsequent divergence of these two populations could have been triggered by any of the following events. First, each population could have been exposed to different external environments with different selection pressures, leading to allopatric speciation in the manner proposed in standard evolutionary theory. Second, both populations may have been exposed to the same novel selective pressures, say, a changed habitat, but only one population, say, the ancestors of the Pongidae, was able to respond with counteractive niche construction by retreating to a still unchanged habitat, while the Hominidae ancestors remained where they were and became adapted to the new environment. Third, both populations may have responded to the same novel selection pressures with counteractive niche construction, but in different ways, each subsequently generating a different array of novel modified selection pressures that fed back on themselves. Fourth, the divergence might have been initated by inceptive niche construction on the part of one population, by which we mean by a novel form of niche construction, initiated by a change in organisms in one population, possibly because of a mutation or a new cultural discovery, which subsequently caused, rather than resulted from, a change in the environment. For example, this might have entailed one population discovering a new habitat or discovering a new form of niche construction, most likely because of the spread of a newly learned behaviour (Bateson 1988; Plotkin 1988; West-Eberhard 1987). Culture, or protoculture, say, on the

Table 1. Niche construction resulting from population genetic processes, information-acquiring ontogenetic processes, and cultural processes, can influence both biological evolution and cultural change (the point is illustrated by a single example in each cell)

Source of niche construction	Feedback to biological evolution	Feedback to cultural change
Population genetic processes	Web spiders marking web or building dummy spiders (Edmunds 1974)	Sex differences in human mating behaviour (Barkow et al. 1992; Daly & Wilson 1983)
Information acquiring ontogenetic processes	Woodpecker finch, by learning to grub with a tool, alleviates selection for a woodpecker's bill (Alcock 1972; Grant 1986)	Learning and experience influence the adoption of cultural traits (Durham 1991)
Cultural processes	Dairy farming selects for lactose tolerance (Feldman & Cavalli-Sforza 1989)	Invention of writing leads to other innovations such as printing, libraries, e-mail

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part of the Hominidae, might have initiated some novel biological evolutionary change (Boyd & Richerson 1985; Feldman & Cavalli-Sforza 1976; Wilson 1985). Fifth, the ancestors of both lineages may have initiated different kinds of inceptive niche construction, again with no key environmental event triggering their divergence.

This enlarged suite of processes operating in hominid evolution raises the possibility that some new traits pay for their own fitness costs through niche construction. One possible example is the evolution of the (large) human brain. The mass-specific metabolic rate of the human brain is about nine times higher than the average metabolic rate of the human body as a whole, but there is no elevated basal metabolic rate in humans that would pay for it (Aiello & Wheeler 1995). Aiello and Wheeler (1995) found that this was possible because the human gut, in particular the gastrointestinal tract, requires fewer energetic resources. They hypothesized that our ancestors could afford a reduction in gut size because they used their brains to improve their diets in proportion to their loss of gut. Aiello and Wheeler suggest that this probably happened in two different episodes of brain evolution, the first coinciding with the appearance of the genus *Homo,* approximately 2 million years ago, and supported by increased meat eating, the second coinciding with the appearance of archaic *Homo sapiens* during the latter half of the Middle Pleistocene and supported by the cultural invention of cooking and, therefore, by the externalisation of part of the digestive processes. This is an example of how a character, the human brain, might have evolved despite fitness costs by paying for itself by its "inventive" niche construction. Big brains would not be adaptive without niche construction.

If niche construction were an important evolutionary agent, then for any clade of organisms it should also be possible to predict a priori which phenotypic traits (which we will call *recipient characters* because they are receptive of selection pressures that have been modified by niche construction) might have been selected as adaptive in environments that have been niche constructed. Pertinent characters, and environmental states, could be measured in populations of closely related organisms that do and do not exhibit this niche construction. It would then be possible to use comparative methods to determine whether a selected recipient character change correlates with a particular niche construction activity, whether the niche-constructing activity is ancestral to the recipient character, and whether the recipient character in question is derived. If we are right, there should be a significant relationship between the pertinent environmental state and the recipient character only when the niche-constructing activity is also present. Because the same logic applies at the cultural level, this method could be applied to hominids, or contemporary human populations, where it may shed light on the relationship between particular genes and memes. For example, in the Kwa, there is a strong correlation between the amount of standing water and the incidence of sickle-cell anaemia only in populations that grow yams. In this case, a cultural practice has left a measurable genetic signature, in the form of a different allele frequency. In theory, it is therefore possible that genetic signatures for other cultural practices, evident in archaeological or ethnographic records, could be identified and used as evidence for the presence or absence of the cultural trait in particular populations or to trace the diffusion of the cultural practice across geographic regions. If so, advances in molecular techniques could eventually aid this line of inquiry.

2.1.2. Rates of evolution. Niche construction may also have influenced the rate of hominid evolution. Much attention has focused on how cultural transmission affects evolutionary rates. Allan Wilson and his colleagues have argued that changes in niche, resulting from complex social behaviour and cultural (or protocultural) transmission, might generate a "behavioral drive," which accelerates morphological evolution by fixing a greater proportion of genetic mutations (Wilson 1985). Wilson notes that there is a monotonic relationship between relative brain size and the rate of anatomical evolution among vertebrates, which he argues is consistent with his behavioral-drive hypothesis. However, theoretical analyses suggest that cultural processes may act both to accelerate and to decelerate evolution (Feldman & Cavalli-Sforza 1976). These apparently contradictory findings make better sense in light of our new perspective, because culture is a powerful medium for human niche construction, and niche construction can both counteract and support evolutionary change. If cultural innovations modify natural selection pressures, then genetic change resulting from modified natural selection is likely to follow. If, as seems likely, the rate of change of cultural niche construction is rapid relative to independent changes in the environment, biological evolutionary rates may be accelerated. Several gene-culture coevolutionary models have found that, because cultural transmission may homogenise a population's behaviour, and because culturally transmitted traits can spread through populations rapidly compared to genetic variants, culture can generate atypically strong selection (Feldman & Laland 1996).

It is widely recognised that culture can also shield genetic variants of low fitness from selection (Boyd & Richerson 1985; Feldman & Laland 1996). For example, improved levels of health care and sanitation are examples of culturally mediated counteractive niche construction that damp out selection against individuals with some gene-related disorders, who may then survive and reproduce in the modified environment. In fact, ontogenetic processes may also damp out selection, as when individuals develop antibodies that counter disease or learn to avoid parasites or predators (Bateson 1988; Plotkin 1988). In addition, the recent culturally enhanced mobility of peoples facilitates greater mixing of genes between populations, eradicating differences and slowing down the divergence of populations. Moreover, a new culturally induced environmental change may be responded to exclusively by a new cultural adaptation. For example, even though smoking during pregnancy probably has a significant effect on the survival rate of offspring, the spread of tobacco smoking is unlikely to select for genes for resistance to smoking-related disease, because advances in medical technology allow smokers and their offspring to survive and because campaigns to prohibit smoking are increasing awareness of its dangers. Under such circumstances, culture is unlikely to affect the rate of genetic evolution.

More generally, organisms have evolved many niche-constructing behaviours that allow them to regulate the environment in such a way as to buffer out particular natural selection pressures. Niche construction that mitigates a se-

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lection pressure may allow populations to maintain greater levels of genetic variation at those loci that would have been affected by selection had the population not expressed that particular niche-constructing trait, because it shields such variation from selection. For example in mammals, genetic variation in the ability to deal with heat through body size or shape of ears or tail, may be exposed to less intense selection in populations that escape extreme temperatures in burrows than in those that do not. However, if the counteractive niche construction breaks down, and, for example, a new predator forces the mammals into the open, the presence of significant levels of variation in genes affecting heat exchange may facilitate rapid genetic evolution. In other words, for specific traits, counteractive niche construction may sometimes facilitate periods of evolutionary stasis, punctuated by rapid genetic change. Moreover, following such change, because the niche construction of many organisms, particularly "keystone" species, modifies the selective environments of other species, subsequent niche construction could trigger a cascade of evolutionary events that realign ecosystems (Jones et al. 1997). Although we do not anticipate all macroevolutionary patterns to be dominated by punctuated equilibria, niche construction does provide a novel, readily observable, and testable microevolutionary process to account for punctuated macroevolutionary trends in particular traits, frequently observed in the fossil record (Eldredge & Gould 1972).

The particular significance of this for human evolution is that, as unusually potent niche constructors, hominids should be particularly resistant to genetic evolution in response to changing environments and, at the same time, capable of dramatic evolutionary change following major innovations. If we assume that hominid niche construction is more flexible than that of other mammals, and that culture enhances the capacity of humans to alter their niches, so that the more technically advanced a culture, the greater its capacity for counteractive niche construction, then a number of hypotheses follow. First, consider Vrba's (1992) hypothesis of "turnover pulses." We would expect hominids to show less response to fluctuating climates than other mammals show. We would also expect more technologically advanced hominids to exhibit less of a response to fluctuating climates than less technologically advanced hominids. Second, consider Bergmann's and Allen's rules (Gaston et al. 1998). These rules suggest, respectively, that populations in warmer climates will be smaller bodied and have larger extremities than those in cooler climates. Again, we would expect hominids to show less adherence to these rules than other mammals. We would also expect more technically advanced humans (e.g., moderns) to exhibit less adherence to these rules than less technically advanced humans (e.g., Neanderthals), assuming that the latter must have been less well equipped than the former to invest in counteractive niche construction. Third, by the same logic, we would expect an inverse relationship between robustness and the capacity for expressing counteractive niche construction. Fourth, it should be possible to reverse the inference, and to use the fossil record to infer something about the niche-constructing capabilities of animals, including hominids. Here we suggest that the greater the phenotypic (as opposed to extended phenotypic) response to environmental change by hominids, the more restricted their capacity for niche construction must have been. We are well aware that some related ideas have been proposed before (see Lewin 1998), but we think our niche-construction perspective could provide a basis for new and much more detailed predictions along these lines (based on a more comprehensive understanding of the underlying processes), and therefore for further empirical work.

2.1.3. The evolutionary roots of culture. Modern culture did not suddenly emerge from some precultural hominid ancestor (Plotkin 1996). The psychological processes and abilities that underlie culture have evolved over millions of years and can often be found in rudimentary form in animals. Cultural inheritance depends on the transmission of learned "knowledge" among individuals by one or more kinds of social learning (Cavalli-Sforza & Feldman 1981; Durham 1991). Hence a first step towards an understanding of the evolution of culture is to consider the evolution of social learning.

During the past 15 years a variety of mathematical analyses have been conducted, exploring the adaptive advantages of social learning, relative to learning asocially or expressing an unlearned pattern of behaviour that has been adapted over the course of genetic evolution (Aoki & Feldman 1987; Bergman & Feldman 1995; Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1983; Feldman et al. 1996; Laland et al. 1996b; Rogers 1988). Despite a plurality of methods, this body of theory has reached a surprising consensus regarding when social learning is expected to be favoured. When environments change very slowly, adaptive knowledge should be gained at the level of population genetics because there are only modest demands for knowledge updating, which can easily be met by genetic systems responding to gradually changing selection pressures. In contrast, when environmental change is very rapid, or when there are sudden environmental shifts, tracking by individual learning should be favoured, as should horizontally (within-generation) transmitted information. In such environments, the genetic system will change too slowly to cope, and social learning from the parental generation is likely to be too error prone, insofar as individuals would pick up outdated information. It is when individuals encounter intermediate rates of environmental change that social learning from parents should be favoured. Here, *intermediate* means when changes are not so fast that parents and offspring experience different environments but not so slow that appropriate genetically transmitted behaviour could evolve instead.

The term *social learning*, as currently applied to animals, describes a ragbag of heterogeneous processes, with a variety of functions, found in a broad array of vertebrate and invertebrate species. A more narrow use of the term would restrict it to those processes that might reasonably be regarded as homologous to processes operating in human social learning and that mediate a general capacity to acquire information from others, regardless of the nature of the information, its function, or the sensory modality employed. Within the narrow category of social learning, humans probably transmit more information vertically from parent to offspring than any other species. Protocultural species typically depend primarily on horizontal transmissions based on social enhancement rather than on imitation or teaching (Galef 1988; Laland et al. 1993). A comparative perspective thus implies that the earliest forms of social

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transmission were probably horizontal. In contrast, humans appear to acquire large amounts of information from their parents, and from the parental generation (Guglielmino et al. 1995; Hewlett & Cavalli-Sforza 1986), suggesting that the lineage leading to *Homo sapiens* has been selected for increasing reliance on vertical and oblique cultural transmission.

The theoretical analyses described above imply that a shift from transient horizontal traditions towards increased transgenerational cultural transmission reflects a greater constancy in the environment over time. Such a shift is difficult to reconcile with the traditional evolutionary perspective because there is no evidence to suggest that environments have become more constant over the last few million years, but rather the opposite. Moreover, even if they had, other protocultural species would also be expected to show more vertical transmission. However, the increasing reliance of hominids on vertical transmission is consistent with our perspective; here, a significant component of the selective environment is self-constructed by the species concerned, and this component could have favoured vertical transmission. We are suggesting that our ancestors constructed niches in which it "paid" them to transmit more information to their offspring. The more an organism controls and regulates its environment, and the environment of its offspring, the greater should be the advantage of transmitting cultural information from parent to offspring. For example, by tracking or anticipating the movements of migrating or dispersing prey, populations of hominids may have increased the chances that a specific food source was available in their environments, that the same tools used for hunting would always be needed, and that the skin, bones, and other materials from these animals would always be at hand to use in the manufacture of additional tools. Such activities create the kind of stable social environment in which related technologies, such as food preparation or skin processing methods, would be advantageous from one generation to the next and could be repeatedly socially transmitted from parent to offspring. It is possible that, once started, vertical cultural transmission may become an autocatalytic process: greater culturally generated environmental regulation leading to increasing homogeneity of environment as experienced by parent and offspring, favouring further vertical transmission. With new cultural traits responding to, or building on, earlier cultural traditions, niche construction sets the scene for an accumulatory culture. This might result in offspring learning higher-order "packages" of cultural traits from their parents, as appears to be the case in preindustrial societies (Guglielmino et al. 1995; Hewlett & Cavalli-Sforza 1986).

Clearly, the transition from animal protoculture to human culture involved much more than a shift towards vertical transmission of information and the development of an accumulatory culture. Nonetheless, it is clear that the new evolutionary perspective portrayed in Figure 2c can generate novel hypotheses that may help reconstruct some aspects of the evolution of human culture.

2.2. Example 2: Human altruism, cooperation, and conflict

At present, standard evolutionary theory provides two principal explanations for "altruistic" cooperation in organisms, kin selection (Hamilton 1964), and reciprocity (Axelrod 1984; Trivers 1985), as exemplified by solutions such as tit-for-tat to prisoner's dilemma-type games (Axelrod 1984). These ideas have been used to account for a lot of cooperation in nature, but neither is sufficient to explain the full gamut of human cooperation (Boyd & Richerson 1985; Richerson & Boyd 1998). Kin selection is restricted to kin, whereas the evolution of cooperation based on reciprocity is probably limited to group sizes of fewer than 10, because increasing the size of interacting social groups reduces the likelihood that selection will favour reciprocating strategies (Boyd & Richerson 1988).[3] It is also hard to account for certain forms of human altruism, such as military heroism, in terms of reciprocity or kin selection (Boyd & Richerson 1985).Our evolutionary framework indicates, however, that the suite of processes that may be regarded as plausible evolutionary explanations for human cooperation is considerably larger than kin selection and reciprocity alone.

We suggest that any organism, O_1, should be prepared to cooperate in ways that benefit any other organism, O_2, provided the total niche-constructing outputs of O_2, or of any of O_2's descendants, modify resources in the environment of O_1, or of any of O_1's descendants, with resulting fitness benefits to O_1 that exceed the cost of O_1's cooperation. This reasoning applies to relatives and implies that cooperation should be more likely among kin that niche construct in mutually beneficial ways and less likely among kin that niche construct in mutually detrimental ways than a strict interpretation of Hamilton's Rule might suggest. The same logic also applies to nonkin. In fact, it is obvious that reciprocal altruism is a special case in which O_1 and O_2 are unrelated individuals of the same species that directly modify each other's environment. Recent analyses suggest that most cases currently described as reciprocal altruism, and many cases of kin selection, are actually forms of intraspecific mutualism that are the incidental outcomes of selfish behaviour (Connor 1995b; Mesterton-Gibbon & Dugatkin 1992). In addition, our statement justifies a variant of reciprocal altruism in which individuals do not trade altruistic acts with each other, but rather an individual aids a second individual if the latter acts in ways that benefit the first individual's descendants.

Mutualisms and commensalisms also fit into this framework. Like altruism, mutualism also depends on the modification of the selective environments of recipient organisms by the niche-constructing activities of donor organisms. However, in the case of mutualisms, O_1 and O_2 are individuals in different species. The same is true of commensalisms, which for our purpose can be regarded as asymmetric versions of mutualism. In commensalisms O_1 cooperates with O_2 because O_2 benefits O_1 by ameliorating O_1's environment, but O_2 is unnaffected by O_1, so O_2 does not cooperate with O_1.

Our general statement sketching the conditions under which organisms should cooperate may, under restricted circumstances, generalise to cases in which O_1 and O_2 are groups of organisms, in one or more species. In many cases, the niche-constructed by-products of several organisms are exploited by a population. For example, shoals of fish, flocks of birds, and herds of animals enjoy reduced predation risks, relative to solitary animals, merely because their combined presence changes the selective environment of each individual (Hamilton 1971). Coordinated fish driving by

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cormorants, or seal hunting by killer whales, provide examples of individuals coordinating their niche construction so that it results in more effective food acquisition for everyone (Connor 1995b).

Mutualistic interactions that result from the exploitation of incidental by-products are more evolutionarily robust than altruistic interactions; because each individual is already acting selfishly, the interactions are less likely to be broken down by selfish cheaters. Organisms may also invest in others to enhance the benefits that eventually return to themselves (Connor 1995b). A large amount of human cooperation can probably be explained in terms of the exploitation and investment in the by-products of others – in other words, in terms of mutualisms resulting from human niche construction. For example, barter and exchange are mutualistic interactions in which individuals or organizations trade products for more desirable alternatives. Moreover, human individuals and institutions "invest," metaphorically, or even literally, in other individuals or institutions to enhance their own returns.

One other possible explanation for cooperation in animals is the revised group-selection hypothesis proposed by Wilson and Sober (1994), about which we have some reservations. In the past, much confusion has been caused by a failure to distinguish between group selection for group or for individual advantage (Wynne-Edwards 1962), or between "replicators" and "vehicles" [4] as the object of group selection (Wilson & Sober 1994). Wilson and Sober maintain that the fundamental question concerning group selection really turns on whether social groups, or any other higher level entities, can be vehicles of selection and not on whether they are replicators. They propose a nested hierarchy of vehicles for genes (individual, group, metapopulation) in which each level also includes a population of lower level units. Selection then acts at the lowest level for which there are fitness differences. Thus, if there are no fitness differences between individuals, there should be a "frame shift" (Wilson & Sober 1994, p. 592) to selection at the group level.

The original, or "naïve" group-selection hypothesis failed, primarily because the processes that maintain group differences and select between groups are typically weak compared to the processes that break down group differences and select within groups (Williams 1966). If group-level adaptations are based on the cooperation of altruists, then any individual who refuses to cooperate can reap the benefits without paying the costs, and selfish strategies should be favoured by natural selection. It is not clear how Wilson and Sober can surmount this obstacle to explain the cooperation of large groups of individuals; they have not proposed any feasible process that could have reduced individual differences within groups, yet promoted differences between groups, during hominid evolution. Here it may be worth reflecting on the fact that group-level cooperation typically depends on niche construction, because group-level adaptations are generally expressed outside of human bodies. Groups may remain cohesive because it pays each individual to invest in mutually beneficial niche construction.

Although we recognize some utility in the replicator-vehicle distinction, and in Wilson and Sober's hierarchical approach, we regard it as a distortion. The entities that are selected, and between which there are fitness differences, are not well described as "vehicles" or even as "interactors" (Hull 1988) but, rather, are "organism-environment systems." Similarly, what is replicated, from one generation to the next is a complex of information (both genetic and cultural) and some environmental (including developmental) resources (Gray 1992; Oyama 1985). Once these distortions are removed, it becomes easier to see how a form of group selection could help account for some human cooperation.

The hypothesis that comes closest to a solution comes from gene-culture coevolutionary theory and places explicit emphasis on culturally inherited niche construction. In this hypothesis, proposed by Boyd and Richerson (1985), group selection works at the cultural level, with group-level cultural traits being selected. The authors place emphasis on a "when in Rome do as the Romans do" conformity, in which individuals adopt the behaviour of the majority. The significance of this "conformist transmission" is that it minimises behavioural differences within groups while maintaining differences between groups. Thus group selection of cultural variation "for the good of the group" is possible because, if an altruistic cultural trait becomes frequent in a cultural group, the transmission process should subsequently discriminate against selfish individuals. Group selection of cultural rather than genetic variation requires a "frame shift" of replicator, because it is not genes that are selected for, but rather groups of individuals expressing a particular culturally transmitted idea. Insofar as cultural selection between groups may favour beliefs that benefit the group at the expense of the individual, Boyd and Richerson provide a new explanation for human cooperation.

Several properties of cultural inheritance, as opposed to genetic inheritance, make Boyd and Richerson's idea attractive. First, cultural inheritance, unlike genetic inheritance, may depend on more than two parents. It is therefore possible for individuals to be sensitive to the most frequent cultural traits in their society and to conform to them. Second, group selection of cultural variants can be faster than group selection of genetic variants, because cultural death does not imply the physical death of all the people in a culture. A threatened or defeated people may switch to the traits of a new conquering culture, either voluntarily or under duress. Thus, unlike Wilson and Sober's group selection, here migration will not weaken the process. Third, symbolic group marker systems, such as totem animals, human languages, and flags, make it considerably easier for cultures to maintain their identities, and to resist imported cultural traits from immigrants, than it is for local gene pools, or demes, to maintain their identity by resisting gene flow (Boyd & Richerson 1985). Fourth, cultural transmission of information about cheaters (e.g., gossip) reduces the efficacy of noncooperative strategies (Dugatkin 1992).

More negatively, conformist transmission may potentially be exploited by powerful individuals, groups, or institutions that dominate the dissemination of information through societies, to promote their own interests. Powerful "cultural parents" may stand to gain from persuading other less powerful humans to conform, perhaps by recruiting extra assistance in modifying environments in ways in which they, rather than the helpers, benefit. These processes may be amplified by tool use, for example, by the technology of the modern media, by weapons, by art, or by deceit. Religious, commercial, and political propaganda, for example,

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can all be used to persuade, trick, or coerce conformity from others against their own individual interests, yet in favour of the interests of a dominant class of cultural transmitters.

We can also reverse our earlier logic to suggest that any organism, O_1, should act in a hostile manner, to the disadvantage of any other organism, O_2, provided the total niche-constructing outputs of O_2, or of any of O_2's descendents, modify resources in the environment of O_1, or any of O_1's descendents, to the detriment of O_1, if the resulting reduction in the fitness costs to O_1 of O_2's outputs exceeds the cost of O_1's agonistic behaviour. It is easy to see how this reasoning might account for a great deal of aggressive behaviour, including a form of reciprocal hostility, in which individuals and their descendents trade antagonistic acts. In other words, we predict that organisms should actively harm other organisms by investing in niche construction that destroys other organism's selective environments, provided the fitness benefits that accrue to the investing organisms from doing so are greater than their fitness costs. Because this is a general idea, it should extend to the human cultural level, with the qualification that at this level other processes may be operating.

2.3. Example 3: Selfish phenogenotypes and multiple-process adaptation

2.3.1. Units of selection in human evolution. A prima facie problem with our multiple-processes-in-evolution approach is that it raises questions about the currency of human evolution. Should cultural traits be measured only in terms of reproductive success, as the sociobiologists advocate, or should they be measured by a cultural transmission rate parameter as well as, or instead of, genes? This problem was one of the earliest hurdles faced by contemporary gene-culture theory. Initially, genetic and cultural processes were treated as independent, with separate fitness scores and transmission coefficients allocated for natural selection and cultural transmission. However, it rapidly became clear that genes and cultural traits can interact in the same way that two genetic loci can interact, to generate associations of genotype and cultural phenotype in nonrandom frequencies (Feldman & Cavalli-Sforza 1984). This means that treating genetic and cultural processes as independent is a distortion. A straightforward, pragmatic solution is to allocate fitnesses and transmission rate parameters directly to combinations of genotypes and cultural traits, a package known as a *phenogenotype.* For example, in Feldman and Cavalli-Sforza's (1989) theoretical exploration of the coevolution of lactose tolerance and milk usage, one phenogenotype was a milk-using individual expressing two copies of the allele conferring lactose tolerance, and another was a nonmilk-using individual with no such alleles. For human sociobiologists, the most appropriate way to think about evolution is from the perspective of the gene: Those characteristics that have been favoured by selection are the expression of the "selfish genes" (Dawkins 1989) that were best able to increase their representation in the next generation. For gene-culture coevolutionary theory, the logic is the same, but the replicator is different: Instead of the selfish gene, there is the "phenogenotype." Those human characteristics that have been favoured in the face of both natural selection and cultural transmission are the expression of the phenogenotypes that were best able to increase their representation in the next generation, by whatever process. As an intuitive shorthand, a phenogenotype can be thought of as a human with a package of genes and experience. In this sense, the phenogenotype approach reestablishes the organism (or rather, classes of organism) as the central unit of human evolution, not as vehicle but as replicator. In fact, what is really replicated is a biocultural complex, with a composite array of information (acquired through multiple processes and stored at different levels) and inherited resources. However, we recognize the need for simple conceptual and formal models that have the utility to explore and shed light on the dynamics of such systems, and we regard the phenogenotype approach as the best method currently available.[5]

2.3.2. Multiple-process adaptation. Controversy has surrounded the sociobiological postulate that human beings typically behave in ways that increase their inclusive genetic fitness (Montagu 1980; Sahlins 1976). It is trite to point out that the processes underlying culture are adaptations and that socially learned information and cultural inheritance may increase reproductive success. Mathematical models that have explored the evolution of social learning reveal that it is a truism of the modelling exercise that the capacity for social learning cannot be favoured unless it generally increases some measure of fitness. Obviously, the same is true of knowledge-gaining ontogenetic processes, so what characteristics of human culture could allow humans to behave in a maladaptive way, or to transmit maladaptive information?

One of the most important findings to emerge from gene-culture coevolutionary theory is that there are a variety of mechanisms by which culture can lead to the transmission of information that results in a fitness cost relative to alternatives. Cavalli-Sforza and Feldman (1981) provided theoretical confirmation of the intuitive notion that cultural traits associated with a viability or fecundity deficit may still increase in frequency in a population if there is strong conversion of individuals to the same trait. Boyd and Richerson (1985) found that, when individuals adopt the behaviour of influential or successful members of their society, maladaptive cultural variants can spread, even if associated with a substantial viability disadvantage. Other gene-culture models reach the same conclusion (Feldman & Laland 1996).

Our perspective suggests that, in each generation, populations of organisms persistently construct or reconstruct significant components of their environments. This means that, as they evolve, organisms may, in effect, drag part of their own environments along with them, thereby transforming their own "adaptive landscapes." If ontogenetic processes, culture, and counteractive niche construction in general have consistently damped out the need for a genetic response to changes in the population's environment, hominid populations may have become increasingly divorced from their ecological environments. At the same time, our hominid ancestors may increasingly have responded to novel selection pressures initially generated by inceptive niche construction and subsequently dominated by cultural traditions. In this case, the common conception that modern human populations are adapted to an ancestral Pleistocene environment (Barkow et al. 1992) can be only partly

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correct. In particular, components of the social environment, for example, traits related to family, kinship, and social stratification may have been increasingly vertically transmitted by culture to the extent that contemporary human populations may have become largely divorced from local ecological pressures. Support for this argument comes from Guglielmino et al.'s (1995) study of variation in cultural traits among 277 contemporary African societies, in which most traits examined correlated with cultural (linguistic) history, rather than with ecology.

In the short term, organisms typically niche construct in ways that enhance their immediate fitness, but in the long term, organisms can also "niche destruct" relative to their own genes. For example, they can build up polluting detritus or strip their environments of resources that are nonrenewable, or too slowly renewing, until they have made their own environments hostile to themselves and to their offspring (Diamond 1993). Among plants, this process typically leads to autoecological succession, whereas animals typically respond by dispersing to other environments. Failure to respond to the feedback from negative niche construction is a possible recipe for extinction.

Could humans drive themselves to extinction? There are two reasons for supposing that this is a possibility. First, culture greatly enhances the human capacity for niche construction. For example, science-based technology is currently having an enormous impact on the human environment. It has made many new resources available via both agriculture and industry; it has influenced human population size and structure via hygiene, medicine, and birth control; it has drastically changed human warfare; it is drastically reducing biodiversity; and it may already have resulted in the degradation of large areas of our global environment. These are all potential sources of modified natural selection pressures. Second, human cultural processes can work much more quickly than human genetic processes, generating new adaptive problems at a faster rate than the human genetic processes can respond to. In these circumstances, human culture might drive either local or general self-induced extinctions.

In many respects, this is a recurrence of an old evolutionary problem. Many relatively long-lived species encounter rates and types of environmental change, whether self-induced or independent, that their genes do not have the capacity to handle, and they frequently become extinct. Clearly, one way in which human beings could adapt to culturally induced environmental changes is through quicker acting responses at some nongenetic level, especially through further cultural change.

Unfortunately, there are well-known snags with this kind of solution. First, the population may not recognise the source of the novel, culturally induced selection pressure. This was the case with the Fore of Papua New Guinea, who maintained a cannibalistic tradition despite the fact that it perpetuated a deadly disease (Durham 1991). Second, the required corrective technology may not always be available, or it may be too costly to introduce. For example, in theory the Kwa could have responded to the increased selection by malaria by the cultural control of this disease, but in fact they lacked the technology to do so. Third, the feedback from cultural niche construction may be indirect, which may make it difficult to recognise any longer term negative consequences of the niche construction. Rogers (1995) documents how the adoption of wet rice cultivation in Madagascar had a range of diffuse indirect effects only manifest several generations later, including changes in tribal government, patterns of warfare, and the role of the father. Fourth, responding to cultural change with further cultural change always risks introducing a "runaway" situation, in which each new solution generates the next problem, at an ever accelerating rate. The phenomenon of antibiotic resistance is a recent example (Ewald 1994).

3. Concluding remarks

In the preceding sections we have begun to develop a new type of evolutionary framework for the human sciences by emphasising niche construction and ontogenetic and cultural processes. We have also illustrated the conceptual model with a number of ideas related to sample topics. Our hope is that these suggestions will encourage others to use the evolutionary framework we are proposing in this target article, either to further develop some of the ideas we have already discussed, to the point where they can be empirically tested, or to generate other hypotheses of their own.

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NOTES

1. Here construction refers to a physical modification of the environment and not to the perceptual processes responsible for constructing a mental representation of the world from sensory inputs.

2. Although in their book, *Genes, mind and culture,* Lumsden and Wilson (1981) labelled their models "gene-culture coevolutionary theory," their approach had more in common with conventional sociobiology than with modern gene-culture coevolutionary theory (Feldman & Cavalli-Sforza 1976; Boyd & Richerson 1985). [See multiple book review of Lumsden & Wilson's book, *BBS* 5(1) 1982.]

3. Boyd and Richerson (1992) established that punishment allows reciprocity to evolve in large groups, if reciprocators respond to noncooperation by withholding future cooperation and also punish others who do not punish noncooperators. However, they also established that there is no guarantee that the cultural traits stabilized by punishment will enhance individual or group fitness.

4. Dawkins (1989) coined the terms *replicator* and *vehicle* to distinguish between the "immortal" genes, which are replicated each generation, and the transient, vehicular organisms that house them. Dawkins also makes the point that there may be other kinds of replicator, for instance, culturally learned beliefs or traits, or "memes," which may be selected by processes analogous to natural selection, a point anticipated by Cavalli-Sforza and Feldman (1973) and central to contemporary gene-culture coevolutionary theory.

5. The "phenogenotype" is simply a convenient tool for operationalizing the modelling of gene-culture coevolution. We anticipate that, in some circumstances, the relationship between genetic information, culturally acquired information, and behavioural phenotype will eventually prove too complex to be handled in this way. For example, in the past, gene-culture modellers have chosen to parameterize the frequency either of a behaviour pattern

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or of acquired information, as convenient. Such switching between symbolically encoded information and phenotype is legitimate only where there is a tight correspondence between information and behaviour (Cronk 1995). Where this correspondence is weak, gene-culture methods might have to be developed further, for example, by introducing a coefficient into the models that represents the extent to which individuals with a particular combination of genes and acquired information are likely to express a particular behavioural phenotype.

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Gene-culture coevolution does not replace standard evolutionary theory

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Abstract: Though the target article is not without fertile suggestions, at least two problems limit its overall validity: (1) the extended gene-culture coevolutionary framework is not an alternative to standard evolutionary theory; (2) the proposed model does not explain how much time is necessary for selective pressure to determine the stabilization of a new aspect of the genotype.

Laland, Odling-Smee & Feldman deserve credit for an original treatment of aspects of the relation between culture and biological evolution. That notwithstanding, their extended gene-culture coevolutionary framework cannot be considered an alternative to standard evolutionary theory, as the addition of the concept of niche construction to the model developed in previous works of Cavalli-Sforza and Feldman (1981) and Boyd and Richerson (1985) is not sufficient for the proposed model to replace the standard approach to the study of evolution. The reason resides in the interactions between the processes of niche construction and natural selection.

According to Laland et al., evolution consists of mutual and simultaneous processes of natural selection and niche construction (sect. 1.1, last para.). In reality, invoking a mechanism parallel to natural selection is redundant. To demonstrate this it is enough to consider three simple examples cited by the authors: migratory behavior (sect. 1.1, para. 2), the behavior of certain insects (such as ants and termites) capable of regulating the humidity and temperature of their nests (sect. 1.1, p. 3), and finally the behavior of earthworms, which changes both the structure and chemistry of the soil (sect. 1.1, para. 9). In all these cases (as in others cited in the target article), the reference to a process able to permit diverse species of animals to choose, modify, and create their own ecological niches is not mistaken; it is in fact useful as it allows the formulation of hypotheses about the adaptation of these species to their environment. But the process cannot be considered as an alternative, nor even as an adjunct to the standard mechanism of natural selection, for at least two reasons. First, because in cases such as migration or the regulatory behavior of ants and termites, the processes of niche construction do not counteract the pressures of selection but are rather its direct expression. To fail to consider this point adequately is to risk inserting a teleological dimension into the explanation of evolutionary phenomena, as if to say that because it is cold at certain times of the year, or because the interior temperature of the nest may rise too high, organisms evolve behaviors to counteract these pressures. In reality, the causal relationship is the inverse; thanks to natural selection, those ancestral organisms that as an effect of random genetic mutation had traits that rendered them capable of particular regulatory behaviors were favourably selected. Inasmuch as it is obvious that Laland et al. do not intend to present a teleological explanation of evolutionary processes, some passages of their work can lead to misunderstandings in this sense.

The second reason to doubt that niche construction and natural selection are two alternative processes can be derived from the example of the earthworms mentioned above. The very fact that some phenotypical characteristics of earthworms have coevolved in an environment that at least partially "niche constructed" by their ancestors, demonstrates that niche construction is simply one of the ways in which natural selection manifests itself. Niche construction and natural selection are therefore not alternative or parallel processes; the former is simply one of the expressions of the latter. In substance, if Laland et al. deserve credit for having investigated the role played in evolution by selective pressures other than purely physical ones such as temperature, humidity, the availability of food, it seems harder to share the idea of assigning the body of selective pressures responsible for niche construction to a process distinct from natural selection. These considerations are even more convincing when the authors refer to more complex examples of niche construction, such as those based on ontogenetic and cultural processes. Even in this case their model cannot be substituted for the standard one, although it does, in a certain sense, provide an amplification.

Furthermore, the very treatment of ontogenetic and cultural aspects puts into greater relief another problem in the work of Laland et al. regarding the time necessary for selective pressure to determine the appearance and stabilization of a new aspect of the genotype. In some sections the authors speak of "enough generations" (sect. 1), and "sufficient generations" (sect 1.1) for an environmental modification due to niche construction to become a selective pressure that can influence a species. There have been similar difficulties in other theoretical frameworks such as the gene-culture coevolutionary theory of Lumsden and Wilson (1981; see also BBS multiple book review: Lumsden & Wilson's "Genes, Mind, and Culture" *BBS* 5(1) 1982). The framework of evolutionary psychology today seems to deal better than any other with the problem of the time necessary for selective pressure to permit the appearance and stabilization of a new mechanism. Evolutionary psychology (Barkow et al. 1992) resolves the problem by examining the selective pressures recurrently encountered over the last two million years (at least) by individuals of genus Homo in their environment of evolutionary adaptedness. By making reference to the type of social organization that has characterized the evolutionary history of genus Homo, it is possible, for example, to develop a hypothesis regarding such a particularly complex behavior as deception (Adenzato & Ardito 1999).

Until the modern gene-culture coevolutionary theory is able to quantify closely enough the time needed for an environmental change from niche construction to effect a *stable* modification in the nature of an organism, we must acknowledge the fact that a new trait evolved in response to that environmental change can quickly disappear, following a sudden cessation of the selective pressure. This is the same as asking whether the persistence of an environmental change due to niche construction for some generations ensures that there will be a stable modification in the nature of an organism.

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Phenogenotypes break up under countervailing evolutionary pressures

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Abstract: The phenogenotype, a routinely co-occuring combination of a cultural and genetic trait, is unlikely to survive over time because of the potentially varying evolutionary pressures upon cultural as opposed to genetic traits. This is because the production and evaluation of cultural inputs will themselves be based on information previously acquired culturally. As a result, treating both cultural and genetic inheritance in a single recursion may be problematic.

The picture of multiple evolutionary processes Laland et al. present is imaginative and provocative. I am a great fan of this work. But duty declares that I must be curmudgeonly. My complaint will center on the notion of a "phenogenotype."

Laland et al.'s assumption is that genetic and cultural transmission proceed so that there is a recurring probability that cultural trait A will be linked with a genotype B. Together, this combination constitutes a phenogenotype. Rules for the recombination of genetic and cultural traits can be recursively applied to these phenogenotypes to describe the genetic-cum-cultural evolution of a population. It is the frequency of these Siamese twins that is traced by Laland et al.'s models. Generally speaking, the models abstract from the complex process by which genotypes are converted to phenotypes or vice versa, for both inheritance systems. There is simply a mapping function in terms of transmission probabilities from pheno- or genotype to pheno- to genotype, one generation to the next.

Laland et al. argue that there are a number of empirical reasons to think such a convergence of cultural traits with genetic ones in each generation is stable and thus amenable to recursive treatment. First, most cultural traits appear to be passed from biological parents to offspring in quasi-Mendelian fashion (Laland et al. 1995). They further assume that the proximate psychological mechanisms directing cultural inheritance – the mechanisms of trait selection and mutation – are largely controlled by genes, so that culture is basically adaptive (sect. 1.3, para. 6).

The fly in the ointment for this argument, I think, is the fact that the bottleneck through which genes and cultural traits are supposed to pass each generation is the brain. Laland et al. accept the basic tenet of evolutionary psychology that there is considerable naturally-selected structuring of the mind. So the mutational forces acting on cultural variants are gene-based. Evolved brain structures should produce a particular kind of cultural mutant – the ecologically rational types which Boyd and Richerson (1985) call "guided variations." And, according to Laland et al., selection of cultural traits can be summarized as biased transmission, due to evolved psychological preferences that reject one cultural variant over another.

But is culture merely a hostage to gene-directed variation, a patsy to natural selection, as the authors suggest? I want to argue that there are *cultural* selectional and mutational forces that have a degree of independence from genetic control, thanks to the peculiarities of the brain as an information processor.

What are these peculiarities? Neuroscience increasingly often shows that plasticity is the name of the game in the cerebral cortex (Merzenich & deCharms 1996). This is true both in terms of moment-to-moment changes in the states of synapses, and the functional "hard-wiring" of the neuronal network itself at somewhat longer time-scales. That is, the long-term storage of information sometimes requires that new synaptic connections be grown (Engert & Bonhoeffer 1999). Indeed, whole new neurons can be produced in some parts of the fully mature brain (Kempermann et al. 1997). None of this directly involves the transcription of genes. Further, "memory" and "learning" use the same substrate: massive neuronal networks (Fuster 1995). Cultural information is not just passively called up from a stable memory store, to be remodeled by an independent processor. The analogy to the hard disk and CPU of computers, popular in cognitive science, doesn't wash at this level. Rather, *all* processing is related to the activation of more-or-less susceptible neurons by hormones and other proteins. Because, in effect, culturally acquired knowledge is part of the brain, some mental machinery is not merely ontogenetic but cultural.

In evolutionary terms, a quite different set of variants may result if cultural traits (memes, if you will) can "do it themselves." Some memes will be created by other memes, and not by gene-derived machinery. Copying "errors" during culture acquisition will be governed by production rules that have not been stamped with natural selection's seal of approval and therefore need not promote fitness.

The same argument holds for cultural selection criteria. Again, the question is whether the psychological biasing that Laland et al. suppose can be based on memetic rather than genetic criteria. And again, I suggest that because the mental funnel through which information must go is partly made of memes, some of the "epigenetic rules" that evolve within an individual's life-span to filter in-coming information will be memetic in nature.

So, memes can evaluate and produce other memes (Dennett 1995). In this way, memes introduce new selectional forces and new kinds of variation into the cultural evolutionary process. Genetic and cultural phenotypes pass through the brain, but not necessarily in tandem, and not subject to the same evolutionary pressures. This suggests there is good reason to suppose that centrifugal forces cause phenogenotypes to fly apart over time.

In addition, the relationship between genetic and cultural inheritance might be sufficiently complex that it cannot be remedied by an easy "fudge factor." No bias term thrown into the author's model could compensate for the improbability of a gene-culture link surviving from one generation to the next. This complexity arises because each phenogenotypic "mating" of a genetic and cultural trait is likely to be differently affected by cultural mutational and selectional forces. Why? Another doctrine of evolutionary psychology is that the brain consists of domain-specific, modularized processors which are the result of natural selection on the brain's decision-making abilities. This modularity results in particular types of content getting shunted to different parts of the brain, where unique algorithms deal with that kind of input. More radically, the algorithms themselves are constantly changing as individuals learn new things (because inputs modify the wiring of brains). If cultural variant A winds up in area 1 but variant A′ in area 2, and memes are differently evolving in these two areas of the brain, then the cultural aspect of mental processing of these two variants will differ. As a result, the relationship of competition between them for linkage to a particular genotype will itself evolve according to memetic rules not discernable in the phenogenotype recursion. So, in fact, there can be an independent cultural component to gene-culture evolution, a double dynamic. Dealing with this complication would be truly difficult using a single recursion equation.

Of course, not all "gene-culture coevolutionary" theory makes use of the phenogenotype concept in order to analyze human evolution. Indeed, most of the models in Cavalli-Sforza and Feldman (1981) or Boyd and Richerson (1985) are restricted to one evolutionary currency (cultural or genetic). But then the problem is that no explicit attention is paid to the dynamic interaction of one inheritance system with the other. Only if you allow that cultural traits are subject to the crucial evolutionary processes using criteria independent of genes do you have real "dual inheritance" (Boyd & Richerson 1985), real gene-culture coevolution. Laland et al. give short shrift to the meme, this partner-in-process to genes.

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Our shared species-typical evolutionary psychology

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Abstract: Because human cultures are far more similar than they are different, culturally constituted niches may work to limit or prevent the development of genetically based psychological differences across populations. The niche approach further implies that we may remain relatively well-adapted to contemporary environments because of the latter's cultural niche continuity with ancient environments.

This is a small comment on one component of a very full and stimulating target article, in accordance with Laland et al.'s goal of "spell[ing] out the repercussions of this perspective [niche construction] for the human social sciences" (sect. 1.1, last para.). The authors suggest that, as our own species evolved in the past and continues to evolve today, we have carried with us and may continue to carry with us a niche constructed of cultural information that partly insulates us from selection pressures emanating from our ecology. As cultures differ from one another, our niches, and therefore the selection pressures to which we are subject, may differ from cultural group to cultural group. Thus, they conclude, the argument that we are "adapted to an ancestral Pleistocene environment can be only partially correct" (sect. 2.3.2, para. 3). In support of this line of reasoning, they cite Guglielmino et al.'s (1995) study showing that in 277 African societies, linguistic history was a better predictor of most cultural traits than was ecology.

But how different are cultural groups and their niches from one another? Ethnographers have long emphasized the exotic and paid scant attention to similarities across cultures. Donald E. Brown (1991), however, argues powerfully that our cultures are far more similar to one another than different. His "universal people" have symbolic systems of communication that include language and taxonomies, they can distinguish between self and other, they have kinship systems that share a number of attributes, they have a system of statuses that are objectified, they excel at toolmaking, they have a system of marriage and also a system of family, the core of which is a mother and her children, the adults participate heavily in the socialization of children, individuals have social identities and have unequal prestige, there is a division of labor based in part on age and sex, they plan for the future, they have a system of governance that includes leadership and rules or laws, they have a sense of ethics, they have hospitality and rituals, they have religious/supernatural beliefs, they have hostilities between ingroups and outgroups, they have a shared worldview and a sense of aesthetics.

If we assume that these similarities give rise to many similar niche-specific selection pressures in all or most societies, we come to the conclusion that culture, rather than only leading to differences across human populations, may also have kept us from diverging significantly (at least as far as the genetic bases of behavior are concerned). The cultural niche likely keeps us together as a species more than it divides us.

Laland et al. do argue that under some conditions, "as unusually potent niche constructors, hominids should be particularly resistant to genetic evolution in response to changing environments" (sect. 2.1.2, para. 4). However, they do not consider the implications of pan-cultural universals in this light, instead placing more emphasis on the continual reconstruction of niches.

Let us assume that our cultures are continuous with those of our Pleistocene ancestors and that the latter shared Brown's universal characteristics: if this assumption is valid, then our cultural niches must include much of our environment of evolutionary adaptedness. To the extent our contemporary niches do retain aspects of Pleistocene culture, then to that extent we may be better adapted genetically to our contemporary societies than some might imagine.

Economic institutions as ecological niches

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Abstract: Economic institutions governing such activities as food sharing among non-kin, the accumulation and inheritance of wealth, and the division of labor and its rewards are human-constructed environments capable of imparting distinctive direction and pace to the process of biological evolution and cultural change. Where differing structures of these institutions take the form of distinct conventions sustained by (near) mutual adherence, small initial differences may support divergent evolutionary trajectories even in the absence of conformist behaviors.

The labor market, as every graduating senior knows, influences what one must do and be in order to achieve material success, rewarding some inherited or acquired skills, physical characteristics, and affective traits with rapid advancement, while consigning the bearers of less marketable characteristics to tenuous employment at the bottom of the occupational ladder (Bowles 1998). By the processes of assortative meeting and mating, persistence in schooling and success in the labor market influence the traits of those with whom one conceives and raises children. The labor market is at once persistent, variegated and wholly of human construction; differences in labor market structures are passed on over generations, and occasionally modified by chance and design. Labor markets are thus a prime case of what Laland, Odling-Smee & Feldman term human niche construction, with likely long-term effects on the process of both cultural and biological inheritance.

The possible influence on biological evolution of culturally transmitted economic practices such as distinct crops and technologies has long been recognized, of course. (Durham 1991; Feldman & Cavalli-Sforza 1989). I extend this reasoning by taking account of the ways in which economic institutions per se constitute a human-constructed environment affecting evolutionary processes independently of the material form of livelihood (for example, the labor markets for auto workers show distinctive national differences, despite the similarity of the technologies involved).

Labor markets, of course, are a relatively recent construction, attaining importance in the early pockets of proto-capitalism only in the last half millennium and in most parts of the world only in the past century, and for this reason to date have had little influence on the gene pool. But other markets and other economic institutions, such as primogeniture, are of more ancient provenance: some, such as food-sharing among non-kin, apparently dating from the late Pleistocene and therefore encompassing 50,000 or more years of human history.

Many economic institutions may be represented as one of a number of possible *conventions,* adherence to which is in the self interest of each member of the population as long as all (strictly, most) of the others adhere as well (Bowles, forthcoming; Young 1996). Examples include simple principles of division such as "finders keepers" or "first come first served," as well as more complicated principles of allocation such as the variety of rules that have governed the exchange of goods or the division of the products of one's labor over the course of human evolution. Conventions, like the practices of driving on the right or on the left, are self-enforcing as it is not individually beneficial to deviate from the convention unless most of the others do as well. It is partly for this reason that conventions are an insightful lens for exploring early human evolution in foraging bands which lacked specialized state institutions for the enforcement of the rules of the game.

The fact that the benefits of adherence to a convention covary positively with the fraction of the population adhering to it bears a number of important implications for the evolutionary role of human niche construction. First, in a group-structured population one would expect to find uniformity within groups (most members of the group adhering to one or the other convention). The reason (as the driving on the right or the left example reveals) has noth-

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ing to do with conformism, and depends entirely on the positive feedback regulating payoffs. Second, small ecological differences and chance events will generate large between-group differences in conventions. Third, while local uniformity and global heterogeneity is likely to persist over long periods of time, a group may "tip" from one convention to another either by chance events or through the deliberate collective action of its members. These three characteristics of conventions motivate my observation that economic institutions represent human-made environments which are both varied and persistent across generations and hence are constructed niches in the sense of Laland et al.

Can these environments affect the process of biological evolution and cultural change? Because economic institutions influence who meets whom to undertake which tasks under which rules of distribution, they map individual phenotypic characteristics into expected material rewards. Economic institutions also affect the degree of intergroup mixing (through trade, conquest, and migration, for example). Thus it seems likely that where these environments are long enduring, affects of economic institutions on both biological and cultural evolution would be anticipated.

As the influence of economic institutions on cultural evolution is not controversial (Bowles & Gintis 1998), I give a speculative but not implausible example concerning the way that economic institutions affect selective pressures operating on traits subject to genetic transmission. Sharing of some foods among non-kin appears to have been a common practice among foraging bands during the late Pleistocene (and hence during most of anatomically modern human existence); this norm of sharing (and contributing to the food to be shared) was probably sustained through various forms of punishment of deviants, ranging from gossip and ridicule to ostracism and execution (Boehm 1993). These arrangements determined a relationship between phenotypic traits and material reward, survival, and consequently fitness (for example, acquiring adequate nutrition depended not only on being a good forager but also on skills relevant to being a group member in good standing. A predisposition for sharing and punishing sharing-norm violators might thereby have been favored [Bowles & Gintis 1999]). In those cases where food sharing was supplanted by food storage, individual accumulation of food stocks and eventually the inheritance of wealth, the mapping of phenotypic characteristics to material reward and fitness was considerably altered.

The importance of economic institutions as a case of human niche construction might also be illustrated by the distinctive selective pressures implied by impartible inheritance as opposed to equal division rules, and other examples too complicated to be developed here. Whether any of these "institutional niches" have had substantial effects on biological evolution cannot of course be determined on the basis of current knowledge.

Can niche-construction theory live in harmony with human equipotentiality?

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Abstract: Consistent with the "niche construction" hypothesis, human beings tailor their behavior to local circumstances in ways beneficial to their inclusive fitness. However, the fact that any human being seems equally capable of adopting any of these context-dependent fitness-enhancing behaviors makes niche construction theory implausible in practice. The human capacity for exhibiting context-specific behavior remains in need of an explanation.

Laland et al. are making the logically plausible case that modifications of their environments brought about by biological organisms create new selective pressures that then set the scene for the genetic evolution of the self-same organisms responsible for altering their environment in the first place. The idea, while it appears to reconcile some problems regarding human action, also raises others.

The "niche construction" hypothesis does seem on its face to explain why human beings living in different cultural settings exhibit different behavior patterns, each of which seems easily explainable as an adaptation, even though many of these cultural settings are very different from our assumed environment of evolutionary adaptedness (EEA). According to standard evolutionary theory, to call such behaviors adaptations is a misuse of the concept of adaptation and a misuse of evolutionary theory because a behavior is an adaptation only if it is a gene-mediated trait selected for in our EEA. Activities that look like good solutions to survival and reproductive challenges not found in our EEA may be adaptive, that is, useful, but they are not adaptations. It is this kind of reasoning to which Laland et al. are responding.

The "niche construction" hypothesis suggests that we may be able to resuscitate the kinds of adaptative explanation to which conventional evolutionary psychologists object. Thus, for example, take the interesting association of avunculocality, in which a maternal uncle raises his sister's son, and permissive attitudes toward sex. Following the logic of Laland et al., avunculocality can be interpreted as an adaptation to the problem of paternity uncertainty (see also Hartung: "Matrilineal Inheritance" *BBS* 8(4) 1985). Where cultures endorse permissive sex norms, a wife may become pregnant by a man other than her husband. A man, therefore, is better off raising his sisters' sons, to whom he knows he is related, than his wife's children, who may have no genetic connection to him at all. Similarly, varying patterns of marriage can be viewed as adaptations. Thus, in the handful of societies that allow polyandry, that is, the marriage of one woman to more than one man at the same time, we find that certain customs regarding subsistence activites and inheritance rules mean that individual men may have difficulty supporting a wife and children on their own. The solution is that they compromise and share the burden with co-husbands. Further, men in such cultures tend to minimize the reproductive cost of wife-sharing by practicing fraternal polyandry. That is, their co-husbands are also their brothers, so that a wife's children, if they are not also those of a particular husband, are his nephews or nieces.

Similar examples of behavior-niche correspondence abound in the cross-cultural literature. In each of these cases, we have a set of variations in human behavior that seems to be adaptively responding to culturally driven variations in environment. How persuasive, though, is the idea that these are genetically mediated adaptations that are the product of changes in selection pressures resulting from culture?

Here is the problem with niche construction theory. Whereas there are numerous examples of cultural variations in human behavior for which we can construct adaptationist stories, I know of no evidence that genetic variations underlie them. That is, there are no data suggesting that men in polyandrous societies carry polyandry genes and men in monogamous societies carry mongamy genes, and so on, for other examples of adaptationist stories. I am not suggesting that it is in principle silly to think that behaviors of this sort could be underwritten by genes. If genes can ground nest-building and courting in birds, web-building in spiders, and language learning in human beings, why not polyandry or avunculocality? The problem, however, is that, if you pluck a baby boy born in a culture practicing polyandry from his homeland and set him down in a community where monogamy is the norm, we all know what happens. The transplanted youngster does not grow up craving a co-husband. So one of the wrinkles that niche construction theory needs to iron out is the inconvenient fact that human beings everywhere do seem to be very much alike with respect to their potential to adopt the entire array of behaviors and cognitive habits that we can find anywhere in the world.

Researchers like Laland et al. are currently constructing mathematical models to represent the kind of genetic evolution in response to niche construction that would underwrite their hypoth-

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esis, and they argue that such genetic evolution is in principle possible. That is fine with me. But whenever we find that the same human being is able to adopt the practices of any human culture, it seems to me that an argument for culturally mediated genetic evolution is hard to sustain. Thus, to take one of the examples of hypothetical niche-mediated gene evolution proposed by Laland et al., if cooperation is more likely among kin who construct niches in mutually beneficial ways than in kin who do not, we would still not expect a baby born in the first kind of culture and immediately displaced to the second to cooperate with kin. The very strong intuition that the same human baby will cooperate or fail to cooperate with kin depending upon local circumstances argues against culturally mediated gene evolution.

How, then, can we explain the uncanny ability of human beings to unthinkingly adapt to local circumstance in ways that seem so consistent with the predictions of evolutionary psychology? Leda Cosmides and John Tooby (Barkow et al. 1992) have proposed that biological organisms are endowed with knowledge-rich psychological mechanisms that underwrite fitness-enhancing behavior. The mechanisms, which are built in by natural selection, are supposed to operate like contingency rules, producing appropriate behavior for particular environmental circumstances. The theory accounts for the kind of flexibility that human beings display in response to local conditions. In this view, all human beings would be endowed with the full array of psychological mechanisms, some of which would then be triggered by the particular circumstances in which a person finds himself. But the theory does not explain how natural selection could select for appropriate responses to circumstances that members of a species have not encountered in the EEA. Perhaps the algorithms are elaborated in particular groups of human beings as they construct new niches, consistent with niche construction theory. But then, why aren't some people stumped about how to behave when they encounter unfamiliar niches?

In short, we are still in need of an explanation of how human beings manage to tailor their behavior to local circumstances in ways beneficial to their inclusive fitness while rarely being consciously aware that they are doing so. Until we have evidence that variations in human behavior tailored to particular niches are actually mediated by gene variation, the niche construction hypothesis isn't up to the job.

NOTE

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Evolutionary simulation modelling clarifies interactions between parallel adaptive processes

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Abstract: The teleological language in the target article is ill-advised, as it obscures the question of whether ecological and cultural inheritances are directed or random. Laland et al. present a very broad palette of explanatory possibilities; evolutionary simulation models could help narrow down the processes important in a particular case. Examples of such models are offered in the areas of language change and the Baldwin effect.

The central theoretical message of the target article is that, through modifying their environment, organisms affect the selection pressures acting on them. The extent to which previous students of evolution have been unaware of this interaction is debatable; for example, orthodox models of coevolution address changes in selection pressure brought about by the evolution of new traits. The novel contribution made in Laland et al.'s target article is simply to note that, to the extent that these new traits affect the environment, they may have additional effects on selection which may persist for longer than the lifetime of an individual organism. Nevertheless, the authors are to be commended for outlining a theoretical framework that makes these matters explicit.

We were somewhat alarmed by Laland et al.'s pervasive use of teleological language in describing the processes of "niche construction." Whilst evolution is clearly an undirected process, and ontogenetic development (including learning) is equally clearly goal-directed, the status of some nascent, intermediate adaptive level is far less straightforward. In their use of terms such as "counteractive niche construction," do the authors mean to suggest that cultural or ecological inheritance should be considered to be purposive after the fashion of individual learning? If so, must there have been natural selection for the ability to construct niches in the same way that there has been natural selection for the ability to learn? The issue is not merely a linguistic one, since we know that very different dynamics are to be expected from directed as opposed to non-directed adaptive systems. Consider that, since mutations in general are deleterious, niches constructed through genetic mutation (e.g., web building by spiders) will be rare success stories among many failures. However, since the fitness consequences of novel learned behaviours may be distributed very differently from those of genetic mutations, and will depend on the specific learning mechanism involved, the success rate of niches constructed through learning (e.g., the learned use of a grubbing tool by woodpecker finches) will differ accordingly.

The interaction between genetic evolution, learning, and intervening adaptive processes will turn on specific facts about genetic constraints, learning biases, and the environment of the organisms involved. Although we appreciate the value of the target article in introducing such a wide range of explanatory possibilities, individual cases demand individual explanations. A move in this direction has been achieved by the emerging field of evolutionary simulation modelling (see Belew & Mitchell, 1996, for examples). This paradigm employs models that simulate the dynamic evolution of a population of agents subject to some adaptive process in order to test theories concerning analogous natural systems. These models stand somewhere between the abstraction of mathematical work and the complexity of the real world. They could be used to expand upon the theoretical framework of the target article, by examining the relative importance of different processes (e.g., genetic evolution, learning, cultural inheritance, and niche construction) in specific cases.

In some evolutionary simulations, there is little room for what Laland et al. refer to as "ecological inheritance," as the environment is wiped clean for each new generation of simulated organisms. However, in other simulations the behaviour of one generation does affect the selection pressures impinging on the next, either because new organisms continuously arrive in an established population, or because the behaviour of adults is recorded in some way and used as part of the environment for their children. An example of the latter is Kirby and Hurford's (1997) model of language evolution. New-born organisms must learn a grammar from a set of utterances provided by the parental generation. Thus the ecological legacy is not the physical environment but the linguistic one: a new organism is born into a world of speakers. Kirby and Hurford use their model to challenge Chomskyan orthodoxy, and show that the "evolution" of the language itself, towards greater parsability, is actually prior to the genetic fixation of the grammatical structure. They have used their simulation to go beyond the general observation that genetic and linguistic inheritances may interact, and shown how they may be expected to do so.

The logic of the target article is based on mathematical models outlined elsewhere (Laland et al. 1996; Odling-Smee et al. 1996). The conclusions that the authors have drawn are no doubt sound, but such mathematical modelling can conceal many implicit assumptions. Another virtue of evolutionary simulations is that, like

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models in artificial intelligence, they force their creator to be explicit in every detail. Consider the work of Mayley (1996) on the Baldwin effect – this effect is very close to the concerns of the target article as it involves an interaction between learning and genetic evolution. Mayley uses an evolutionary simulation to demonstrate that the conditions under which the Baldwin effect will result in the genetic fixation of a learned trait are not straightforward. The costs as well as the benefits of learning, and the correlation between genotypic space and the space of behavioural strategies, must be taken into account. Earlier authors had certainly looked at the costs and benefits of learning, but had tended to assume that genotypic and phenotypic space were in perfect correspondence. Such complexities are often glossed over in the kind of abstract mathematical model constructed by Laland et al., yet they remain of great importance to those interested in understanding specific evolved phenomena.

Finally, at one point Laland et al. note enthusiastically that, given their framework, "the suite of hypotheses about . . . evolutionary change is considerably enlarged" (sect. 2.1, para. 1). We would remind the reader that an essential task in science is to *reduce* the number of hypotheses that are plausible with respect to a given phenomenon; we believe that building evolutionary simulation models can help to achieve that.

Evolution, the criterion problem, and complexity

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Abstract: Cultural and dual-inheritance models of evolution present ambiguities not typically present in biological evolution. Criteria and the ability to specify the adaptive value of a trait or cultural practice become less clear. When niche construction is added, additional challenges and ambiguities arise. Its dynamic nature increases the difficulty of identifying adaptations, tracing the causal path between a trait and its function, and identifying the links between environmental demands and the development of adaptations.

An appealing feature of evolutionary theory is that it does not have a criterion problem. Unlike psychologists who struggle with identifying a basis for making judgments about performance (e.g., Austin & Villanova 1992), evolutionary biologists and psychologists have a generally accepted currency for judging performance: survival and reproduction. By the same token, assessing the value of a trait is reasonably straightforward: whether it *contributes* to survival and reproduction (Buss et al. 1998).[1] Theoretical and methodological advances in the life sciences now make it possible to formulate reasonably convincing explanations about the adaptive value of some traits (e.g., Perussé 1993). However, with cultural evolution and dual-inheritance models, units of analysis, criteria, and the ability to specify the adaptive value of a trait or a cultural practice become less clear. Additional challenges arise by integrating niche construction into evolutionary dynamics. It not only exacerbates the criterion problem, but specifying the links between a trait or cultural practice and its function in an organism or social system becomes increasingly complex. In addition, the dynamic effects of niche construction increase the difficulty in drawing connections between environmental characteristics and the evolution of traits. Evolution has typically been considered a relatively "simple" process that produces complex design (Dawkins 1986); however, if niche construction is indeed integral to the evolutionary process, then complex processes may be as much a part of evolution as complex design.

The criterion problem. By what criterion should we judge the adaptive value of a cultural practice? Laland, Odling-Smee, & Feldman suggest that practices retained by a culture "would usually be adaptive" (sect. 1.3, para. 6). Although *use* is a good starting point, it presents problems. What is the appropriate time span for evaluating the use of a cultural practice – short term or long term? Social systems are characterized by complexity, loose coupling, long causal chains, and ambiguous feedback. Therefore, the effects of a cultural practice on the viability of a social system (or gene pool) are difficult foresee (Colarelli 1998; Mealey 1995). While the short term effects of a practice may result in adaptive outcomes, its long term consequences may produce dysfunctional outcomes (e.g., niche destruction through cumulative environmental degradation; Boyd & Richerson 1985). Measurement, tracing casual links, and functional questions are usually much easier with short term criteria. However, because cultural practices reproduce, manifest themselves, and change differently from biologically based traits, short term criteria are a mixed blessing.

The time lag between cultural and biological evolution ratchets up the criterion problem, particularly when a practice's use (or lack thereof) is due to a mismatch between a novel environment and an ancient adaptation. Because biological evolution proceeds at a slower pace than cultural evolution, the retention of some cultural practices occur because of a mismatch between a culture and biological dispositions that evolved in previous environments. The use of psychoactive drugs, for example, stems from their effects on ancient brain mechanisms related to emotion; the drug bypasses evolved control mechanisms and "indicates, falsely, the arrival of a huge fitness benefit" (Nesse & Berridge 1997, p. 64). A similar mismatch contributes the widespread consumption of junk food. On the other hand, some traits may inhibit the use of cultural practices that may be adaptive in current environments. Our interaction patterns in small groups, preferences for face-to-face information about people, and comfort with frequency-type data, are probably based on psychological mechanisms that evolved during the Pleistocene, when the small group was the primary human social unit and humans dealt with relatively small numbers of people and things. For example, although male dominance hierarchies were functional in our hunter-gatherer past (e.g., for warfare and hunting large animals), they often preclude behavior that is adaptive in complex, technologically-advanced societies (e.g., active female participation in mixed-sex groups; Colarelli et al. 1999). Similarly, our evolved information preferences impede the use of statistical information, which can be adaptive in large, complex organizations (Moore 1996). Thus, the relationship between base rates of cultural practices and their adaptive value is not straightforward.

Complexity. Niche construction introjects more instability and uncertainty into the evolutionary process. Such a complex, interactive evolutionary process increases the difficulty of identifying adaptations. First, identifying a singular criterion – as the evaluative underpinning for an adaptation – is less straight-forward. Second, tracing the causal path between a trait or cultural practice and its adaptive functions becomes problematic. And third, adaptive congruency between levels is less likely (Colarelli 1998). Tracing connections requires reasonable certainty about means-end connections. However, in complex, dynamic environments, congruence between design and function is less clear cut, particularly with respect to cultural phenomena. Where niche construction is involved, highly determined models of causal pathways between traits and adaptiveness in complex systems may be unrealistic. Thus, its complexities may necessitate the use of computer simulations as a requisite methodological adjunct to field work (cf. Holland 1995).

The complex interactions among niches, culture, and genes also increase the difficulty of identifying links between environmental demands and the development of adaptations. To what extent do niches stay stable long enough to influence a gene pool? While the niches that produced lactose tolerance and the gene for sickle cell anaemia are good examples of stable, enduring niches, how widespread and robust are such phenomena? Since culture evolves

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more quickly than gene pools, it would seem that few human niches remain stable long enough to influence a gene pool in significant ways. Niche construction also has implications for how we think about the stability of the human environment of evolutionary adaptedness (EEA) and the length of time it takes for human adaptations to evolve (Thornhill 1997). Was the EEA a relatively consistent environment, or was it melange of highly differentiated niches? Did most of our current adaptations evolve in naturally occurring niches and take many thousands of years to evolve, or did niche construction play a significant role and speed up the process (e.g., Durham 1991)? The part of niche construction in human evolution is all the more salient as we become capable of engineering reproduction and development. Advances in medical technology combined with cultural preferences shorten the half-life of the evolution of traits, and they increase instability within current environments of adaptedness.

Laland et al. raise the specter of human extinction from failures "to respond to the feedback from negative niche construction" (sect. 2.3.2, para. 4). Although this is a possibility, the complex evolutionary dynamic they describe could also be viewed as a *variation generator.* "Mistakes" and "errors" that occur in constructing, and responding to feedback from, niches could be adaptive for generating variation in complex systems. Loose coupling, ambiguous feedback, and resultant errors generate variation for adapting to change and act as safety valves to derail potentially destructive runaway processes.

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NOTE

1. I use the term "trait" in the broad sense to mean any heritable physiological or morphological characteristic or fixed action pattern of an organism.

The interwoven conceptual matrix of the cultural replicator

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Abstract: The capacity for flexible niche construction increases suddenly and dramatically when discrete memories and sensorimotor associations become woven into an interconnected worldview. Ontogenetic learning is as vital to culture as social learning because it is the wellspring of cultural novelty. Human altruism may result from pressures exerted at the level of cultural rather than biological replicators.

Laland et al. provide many interesting examples of the important evolutionary consequences of niche construction in both animals and humans. It should be pointed out that this topic is not new to artificial life, or cognitive science, or more qualitative approaches (though not under the name "niche construction"), although it may be new within the tradition of the mathematical models of culture cited here. The advantages of precision and predictability conferred by these mathematical models are bought at the considerable price of sidestepping the distributed, relational processes through which memes are stored and evoked. The assumption that these processes can be swept under the rug is even less valid for culture than for biology (and the quick fix proposed in note 5 will not solve the problem) because memes (unlike genes) are generated on the fly on a regular basis. Thinking is an ever-creative process; no two instantiations of a meme are ever the same. This target article neither builds on the mathematical work it cites, nor does it reach beyond the limitations of this approach to address the highly contextual, strategically creative thought processes that underlie human niche construction. But it does draw attention to the topic, and argues convincingly that it be addressed seriously.

Laland et al. assume that the capacity for niche construction, and culture in general, differs in animals and humans by degree only: "Modern culture did not suddenly emerge from some precultural Hominid ancestor (Plotkin 1996). The psychological processes and abilities that underlie culture have evolved over millions of years and can often be found in rudimentary form in animals" (sect. 2.1.3, para. 1). There is evidence, however, that a vast gulf separates the cognitive abilities of humans from other animals (Donald 1991a; 1993). True, animals modify their environments in useful ways. The phenomenon is even more widespread; a river carves out an ever wider river bed, which in turn "gives it more room" to flow. Since niche construction is come by rather easily, it is probably not an ideal litmus test for ability to engage in the abstract, relational thinking that generates the complex artifacts, languages, theories, stories, and so on comprising human culture. Laland et al. view niche construction as the cornerstone of a new paradigm in evolutionary thought; I view it as one facet of the increased behavioral contextuality conferred when disjoint memories and stimulus-response associations transform into an interconnected conceptual web, or worldview, so that related concepts are connected by way of abstractions [Gabora 1998]. As I see it, the most promising new paradigm in evolutionary thinking is to take seriously the perspective that culture is a second evolutionary system.

Although Laland et al. speak not of cultural *evolution,* but of cultural *change,* they do not address the process by which culture changes, considering only the process by which a change, once in existence, spreads to others. In fact, they equate culture with social learning, which they contrast with ontogenetic learning. But surely ontogenetic learning is as vital to culture as social learning. Ontogenetic learning is the wellspring of cultural variation; there has to be something worth transmitting before social learning will even manifest itself. (In Meme and Variations [Gabora 1995], a computer model of cultural evolution, when I set the agents' ability to imitate to 1 and their ability to invent to 0, what happened was: nothing.) The more often a meme has been socially transmitted, the more time it has had to become adapted to a particular memetic niche, hence the less likely that it will undergo further modification (and thus contribute to cultural novelty). Furthermore, social and ontogenetic learning are impossible to disentangle. For example, under Laland et al.'s scheme, if a child learns from its mother how to peel a banana, this counts as a cultural process. But if it learns how to peel the banana from a cartoon monkey on TV, does this count as an ontogenetic process? What if it gets the idea by watching the petals of a flower unfold? Since the same meme results in all three cases, it seems useful to put them all in the category of cultural processes (with social and ontogenetic components of varying degrees).

Laland et al. explicitly support the notion of memes (note 4), yet they explain behavior exclusively in terms of genetically driven selection. If genetic replicators can have a huge effect on behavior, why not cultural replicators? The fact that new memes regularly take root and die within a single human generation suggests that selective pressures operating at the level of their bearers' survival are not the only selective pressures at play. Laland et al. suggest that in human altruism "it is not genes that are selected for, but rather groups of individuals expressing a particular culturally transmitted idea" (sect. 2.2, para. 9). Isn't it simpler to posit that selection is taking place not at the level of groups of individuals, but at the level of memes themselves? Heylighen (1992) suggests that memes, like genes, exert pressure on individuals to behave altruistically toward others who share them (the equivalent of kin selection for memes). Intuitively this makes sense; we are more inclined to be nice to those who share our ideas than those who share our eye color of blood type. This more direct explanation of human altruism should at least be considered.

Despite these reservations, I believe Laland et al.'s target article raises some provocative issues and makes many excellent points.

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Niche construction, social co-construction, and the development of the human mind

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Abstract: Laland et al.'s model of human evolution and cultural change needs to incorporate theory and research in human psychological development. The psychological approach that focuses on sociocultural contributions to growth offers a way of thinking about individual development that would complement and extend this model.

In Laland, Odling-Smee & Feldman's evolutionary approach to human development cultural change, defined by niche construction and ecological inheritance, is emphasized. The authors describe ways in which human experience, transmitted via culture, can affect both the process and rate of human evolution. In so doing, they hope to integrate the biological and human social sciences. This is an important goal and the theoretical arguments presented are productive steps in this direction. Nevertheless, this goal will not be met unless the biological and evolutionary approaches are better integrated with theory and research in human psychological development.

Psychological development involves the adaptation of the human mind to the circumstances in which growth occurs. The remarkable coordination between basic biological capabilities and the social and cultural context of development is essential to survival, and it is far from coincidental. These constituent elements of human development – the biological, the social and the cultural – "grew up" together over the course of human history (Donald 1991; see also multiple book review, Donald's *Origins of the Modern Mind*, *BBS* 16(4) 1993). The key question that arises from this is: How, over the course of human development, does culture become part of individual functioning?

To answer this, the sociocultural approach to psychological development assumes that intelligent human action is mediated by cultural tools, signs, and symbols (Wertsch 1998). Though this premise is relatively new to contemporary psychological theorizing, it is not without precedent, being largely inspired by the earlier writings of many scholars including the Russian psychologist L. S. Vygotsky and the American educator John Dewey (Cole 1996). According to this view, human development is the process by which children come to understand and participate in culturally organized ways of thinking and acting.

The strength of Laland et al.'s argument is its biological and evolutionary analysis. What is missing is the critical examination and incorporation of the human psychological contributions into the process they describe. In the present model, culture is described as a process in which the only changes that occur are either external to the organism, such as environmental pressures, or internal to the organism but not under the organism's control or awareness, such as genetic inheritance. We know from psychological research, however, that humans are goal-directed organisms who actively participate in the environments in which they live. Of particular importance is the role that the human mind plays in this complex process. I am speaking here of the mind as a symbol generating, meaning-making, artifact-devising, socially transmitting system that is simultaneously an individual, social, and historical (cross-generational) phenomenon. These unique generative properties of the mind are central to the evolutionary processes described by Laland et al. The ability to develop and transmit knowledge and meaning is a hallmark of our species. It is a crucial factor in how people construct, select, alter, and, in some cases, destroy their ecological niche.

Cultural knowledge is transmitted to children in myriad ways, through the activity, goals and values of the culture and its members, the material and symbolic tools that support thinking, and informal and formal social practices, institutions, and routines (Gauvain 1995). Adults play key roles in this process as they encourage and support ways of thinking and acting in their interactions with children. Children play an active, directive role in this process as their developing capabilities, interests, and goals set the stage and boundaries for development in sociocultural context. Thus, through social transactions, children and adults co-construct understanding and this fosters the development of children's thinking and acting along culturally desired lines.

From a psychological perspective, human development is underspecified in Laland et al.'s model. In addition, when psychological development is discussed, the conceptual framework used to characterize its link to culture is social learning. Unfortunately, the principles of social learning included in Laland et al.'s proposal, such as association, reinforcement, and modeling, are inadequate to describe the psychological and developmental aspects of the complex individual, social, and historical process I outline above. In large part this is because a social learning approach assumes that the human organism is a passive, mindless creature. However, neither adults nor children participate in culture in the mechanistic, unthinking way implied in social learning models of development.

In sum, what makes culture and cultural learning such powerful forces in human development, and perhaps in human evolution, is that the course of human development is socially co-constructed through the interaction and shared thinking of more and less experienced cultural members. Social co-construction is instrumental to human culture and its maintenance. In addition to preserving valued cultural practices, it helps ensure that culture is "owned" by new members. That is, as new members help create culture through their participation in it, they shape it in ways that meet their own interests, needs, and goals. Thus, culture becomes part of each individual's nature. This in turn enhances individual connection to and investment in culture. The view of psychological development that I have briefly described is consistent with Laland et al.'s but extends it by addressing: (1) how and why humans participate in niche construction in local time and space, (2) how these local experiences connect to longer-range cultural processes and products, and (3) why individuals are motivated to participate in culture and cultural change.

Niche construction in biological and philosophical theories

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Abstract: I distinguish different versions of the "niche construction" idea. Some are primarily scientific, while others are more philosophical. Laland, Odling-Smee & Feldman's is mostly scientific, but given that fact, there are some changes they could make to their account. I also compare the target article to Lewontin's classic 1983 paper.

Laland, Odling-Smee & Feldman hold that the best way to approach a key set of problems in evolutionary theory is to use a conceptual structure that gives an important role to "niche construction." Standard versions of Darwinism treat organisms and environments as connected by an asymmetric causal structure. The environment, acting through natural selection, affects the composition of biological populations (the left-to-right arrows in Fig. 1a of the target article), but organisms do not significantly af-

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fect the environment. In his classic 1983 paper, Lewontin refers to this standard view as containing an "alienated" conception of the organism. Laland et al., like Lewontin, propose that this asymmetric view should be replaced, at least in some contexts, with a more symmetrical picture (Fig. 1b).

Some defences of niche construction appear to implausibly interpret standard views as denying that niche construction happens. Laland et al. do not give such an interpretation, but it is worth taking a moment to spell out, more fully than they do, how best to treat this question. It is plainly no part of standard neo-Darwinism to deny that organisms modify their environments in myriad ways. Any such denial would be absurd. But standard views can reasonably be taken to claim that these phenomena are inessential to our understanding of how evolution works. Niche construction is treated as mere detail. Any scientific theory must do this type of thing; any scientific theory must relegate much of the causal structure of the world to the status of background or detail. Without idealization of this type, science would grind to a halt. So standard versions of neo-Darwinism are best seen as accepting that niche construction happens, but denying its theoretical importance. Writers such as Lewontin (1983), Gray (1992), and Laland et al. argue that this is a mistake.

But writers in this camp differ on how niche construction, or the "construction of environments," should be understood. I suggest that constructivist views in biology tend to serve two distinct theoretical purposes. One is scientific; advocates of niche construction are arguing for the empirical thesis that niche construction has a causal role that strongly affects how evolution works in some key set of cases. Another purpose is more philosophical; here the aim is more to re-interpret and better understand biological causation in general.

Lewontin's 1983 paper must be seen as directed at both these goals, and I would say the philosophical goal is dominant in that discussion. I see Laland et al.'s paper as different in this respect, as it is primarily directed to specific empirical problems.

How does one tell the difference? One way is to see how broadly a discussion conceives of the relation of "construction." In some discussions, the term "construction" is used so broadly that almost any relationship between an organism and an environment can be described as involving it. Then the aim of the discussion must be to re-orient our general thinking about causation in biological systems, or perhaps in all systems. Lewontin's defence of a "dialectical" view of causation is an example. (By placing some discussions in the realm of "philosophy" I do not mean to deny their importance.) In other works, the relation of construction is conceived much more narrowly, as something that will be found only in some empirically determined set of cases. Then the argument is more scientific than philosophical.

Where does Laland et al.'s treatment fit? I think there is a slight tension between their initial account of niche construction and the examples given in the body of the paper. They say that niche construction refers to the activities of organisms through which they "define, choose, modify, and partly create" their niches (sect. 1.1, para. 1). The four verbs here pick out relations that are very different in status. To "modify" and "partly create" a niche involves, I take it, physical interaction which changes the intrinsic structure of environmental conditions. That is something that only happens in some cases, and happens to a greater or lesser extent. But for an organism to "define" its niche is a very different matter. If "defining" a niche is sufficient for niche construction, then every possible organism constructs its own niche. For all this can mean is that an organism's own biological properties figure in the specification of which aspects of its environment constitute its niche.

In Lewontin's 1983 paper, a very broad conception of "construction" was given, in which physical modification of the environment was not required. Organisms are taken to "construct" their environments in cases where the organism's own properties make some environmental conditions relevant and other conditions irrelevant. This broad conception of "construction" is one reason why I see the aim of the paper as largely (but not exclusively) philosophical; Lewontin is trying to reorient our most general habits of thought about relations of dependence and independence in nature.

Given Laland et al.'s empirical orientation, they would seem better off with a narrower construal of "niche construction." "Defining" and "choosing" should not count; they should only count cases where there is physical modification of the world by the organism (as, indeed, their own Note 1 suggests). All the important examples discussed in the paper would pass such a test, and the rich set of examples is what drives much of the argument.

If niche construction is understood in this narrower way, a slight modification of their diagrams might be appropriate. Given the typical nature of cause and effect relationships, and given the authors' examples, it is generally or often the environment at $t + 1$ that is altered by the organism at t. Some effects that organisms have on their environments will certainly take place rapidly enough to influence current processes of selection. But the missing diagonal arrow from the organism at t to the environment at $t + 1$ is surely an important part of their story.

Another frame shift: From cultural transmission to cultural co-construction

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Abstract: Laland et al.'s bidirectional model is a welcome starting point that can be enhanced by a full incorporation of systems thinking into its framework. Systems thinkers note that culture is not transmitted linearly in chunks but is co-constructed within subgroups. Niche construction, particularly among primates, should be studied primarily through the effects that social relationships have on selection pressures.

Laland, Odling-Smee & Feldman's highlighting of the bidirectional nature of biology and culture comes at an auspicious time. Biologists and anthropologists alike are assaulting the continuing polarization of genes and behavior, and of biology and culture. For far too long, what Gottlieb (1997) calls the "feedupward influences" of genes upon behavior have been highlighted at the expenses of the "feeddownward influences" of behavior on genes. Yet, bidirectionality alone is not sufficient to understand how biology and culture interact. Genes and behavior form a fully coactional system (Gottlieb 1997). Because of this, as the anthropologist Ingold (1998a) insists, even "complementarity approaches," those that speak of "biosocial influences," fail to explain that processes of development, for example, how a child learns to walk, are at once wholly biological and wholly cultural.

Laland et al.'s target article, which does incorporate some elements of systems thinking such as feedback cycles, can be strengthened by fully embracing a systems perspective. The frame shift engendered by a focus on systems thinking takes us away from an exclusive focus on linear social learning (horizontal or vertical transmission) and cultural transmission towards a consideration of how dyads and groups of organisms learn and co-construct culture in distributed ways. My examples will involve primates, but the ideas noted are broadly applicable.

Laland et al.'s argument stresses continuity of behavior across taxa. By demonstrating that niche construction is both general and pervasive, they support the claim that culture is "merely the principal way in which we humans do the same thing that most other species do" (sect. 1.2.3, para. 2) This approach dovetails with, and nicely extends, recent emphases on evolutionary continuity between nonhuman primate and human culture (Boesch & Tomasello 1998; McGrew 1998), and primate communication

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and human language (King 1994; 1999b). An important innovation by Laland et al. is their suggestion that the key evolutionary significance of niche construction rests with the role of feedback; the organism transforms its "adaptive landscape" not only by the direct action it takes, but also indirectly via feedback (sect. 1.1, para. 11).

For many animals, including humans and their closest living relatives the monkeys and apes, the "adaptive landscape" includes family members and/or other social companions. This point is nowhere excluded from or contradicted by Laland et al.'s definition of niche construction or their overall framework. The authors discuss the role of parents and maternal inheritance for many species (sect. 1.1, para. 8) and, when talking about hominids and humans, they highlight social transmission across generations, even mentioning cases of group-level adaptation and cooperation (sect. 2.2). Missing, however, is a full appreciation for the socially constructed nature of learning and culture among dyads and groups, an appreciation that leads in turn to the view that learning and culture are co-constructed.

Natural selection pressures are modified not only by individuals transmitting chunks of knowledge, but by far more complex interactive processes that themselves involve systemic feedback (Ingold 1998b). Knowledge resides in social interactions, and as such it is those interactions themselves that alter selection pressures. Until we look closely at how dyads as dyads and groups as groups are capable of modifying the environment – not merely through the individuals cooperating with each other in a linear additive fashion, but through the emergent properties of the relationships themselves – we will not fully understand niche construction, especially as carried out by complex social organisms.

To see this more clearly, let's consider a well-known behavior of West African chimpanzees. As they grow up, these apes gradually learn to crack open hard nuts using hammers of wood or stone and anvils. Older apes, usually mothers of the infants and juveniles who are learning the nut-cracking, facilitate in a variety of ways the acquiring of efficient tool-using skills by the immatures (Boesch 1991). But the mothers do not "transmit" these skills as they would hand over ripe fruits during food-sharing; their input interacts with the idiosyncratic skills, abilities, and prior experiences of the immatures. The tool-using behavior is co-constructed across the generations (see King 1999a), and in so doing selection pressures are altered.

Even subtle social interactions may have important evolutionary consequences in the sense intended by Laland et al. Patterns of communication in apes are also co-constructed across the generations. My study of gestural communication during an infant female bonobo's first 17 months of life, carried out at the Language Research Center, George State University, provides a case study to illustrate this point. The members of this infant's bonobo family used patterned sequences of behavior that repeatedly unfolded in consistent (although not invariant) ways and that assisted in the emerging communicational competence of the infant. The infant gradually became a more active participant in these patterned sequences, and a more capable gesturer. The quality of her actions changed as she became increasingly able to coordinate them with the actions of others, and as she became a full partner in the kind of interactional synchrony that we know characterizes caretaker-child interactions. If these findings are representative of what wild apes do (and there is good reason to suspect so; see e.g., van de Ritj Plooij & Plooij 1986), they hint at intriguing ways in which apes may affect selection pressures through niche construction.

The watershed proposed by some primatologists (Byrne 1995) to exist between monkeys and apes in various aspects of cognition and communication may extend to the degree of interactional synchrony in communication. [See also Whiten & Byrne: "Tactical Deception in Primates" *BBS* 11(2) 1988.] If apes were the first primates to reach a new level of coordination through communication (see Savage-Rumbaugh et al. 1998), and if Laland et al. are right about the accelerated pace of evolution following major innovations (sect. 2.1.2, para. 4), we might begin to think in a new way about modelling change in the early hominid lineage. We might focus less on whether particular gestures or vocalizations of nonhuman primates are precursors of particular hominid gestures or words, and more on whether the coordinating role of communication in apes could be a precursor to the coordinating role of language in hominids. Speculation aside, however, we can be confident that the emergent social behavior within relationships does alter natural selection through niche construction.

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Big brains as shelters for odd genes: How fast does complex behavior evolve?

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Abstract: Laland et al. suggest that as a specific evolutionary force niche construction has entailed the encephalization of the brain. While not denying rapid co-evolution of brain traits and abilities with niches and cultures, I argue that encephalization reflects a classical genetic buffer system allowing rapid evolutionary adaptation independent of the nature of the selective pressure.

I sympathize with the idea of fast and dynamic co-evolution of biological organisms, niches, and cultures as outlined by Laland et al., but hesitate to embrace the emphasis on the role of niches. Not being an evolutionary theorist, I wish to judge neither the uniqueness of the proposal nor its common points with other concepts. As a specialist in neural and behavioral genetics, however, I see in this and many related concepts the same unanswered question which I raised in a *BBS* commentary 20 years ago (Lipp 1970): How fast can the mammalian brain adapt genetically? The tentative answer given then was: extremely fast.

If so (and there are now theoretical and experimental reasons to believe it; see below), the problem is to conceptualize the importance of natural selection pressures created by niche construction and the speed with which behavioral, neural, and eventually physical adaptations occur. Laland et al. address this point under section 2.1.1, Processes of human evolution, paragraph 2 in which they state that "Big brains would not be adaptive without niche construction" and under 2.1.2, Rates of evolution, in which they refer to A. C. Wilson's work on rates of anatomical evolution and encephalization. Combining the two points, they conclude that niche construction both accelerates and stabilizes human biological evolution, depending on a variety of conditions. This is perhaps true, but the supporting arguments given do not seem convincing. I have proposed elsewhere a model which obviates the need for many of the theoretical arguments used by the authors (Lipp 1989; 1995).

First, in evolutionary terms, encephalization is not a special hominid property but a fundamental biological innovation which enabled mammals and birds to adopt an evolutionary strategy in which genetic variation was accumulated and stored in individuals rather than in populations, as contrasted with strategies (such as of insects) which produce large numbers of individuals with few mutations. Thus, the more encephalized a species, the higher is

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the capacity of the brain to preserve genetic variation, and with it, the evolutionary plasticity and speed of adaptation needed to overcome evolutionary drags such as long life-spans and less offspring. On the other hand, the evolutionary appearance of cognition and intelligence and with it niches, protocultures, and cultures is in principle a (useful) derivative of a genetic buffer system only.

In short, this view is based on how mutated genes affect the development of brain and behavior in an individual, and how such alleles are eliminated by natural selection. The key notion is the visibility and predictability of the mutation at the behavioral level. As evident from experiments with transgenic mice, such visibility is masked by a powerful array of mechanisms subserving brain plasticity, for example, system homeostasis, developmental reorganization, structural adult plasticity, and cognition and learning. The impact of these buffer systems varies during brain development, however.

In the early stages of brain development, mutations affecting cell development or homeotic layout are either lethal or are compensated fully by other genes. During a middle period, characterized by the formation of connections and species-specific circuits, behavioral effects are most strongly masked, because the mutation effects can be altered by all buffer systems. During the last postnatal period of brain differentiation, characterized by differentiation and maturation of the so-called cognitive circuitry of the forebrain, overall buffer capacity is considerably reduced because developmental reorganization is no longer possible. Hence, genetic variation of the CNS is most visible and predictable in higher mental functions.

The effects of natural selection on CNS mutations depend on selective pressure. If pressure is low, mutations of late-acting genes are tolerated because they affect biological fitness and reproduction only marginally. They thus tend to accumulate in such periods, in parallel with mutations in other developmental endpoint genes encoding for variations in pelage, color, and physiognomy. CNS mutations affecting the middle period of brain development remain invisible to natural selection processes, which also favors accumulation. Mutations affecting basic CNS components will be eliminated, and these remain invariant through long evolutionary periods. With increasing selective pressure, late-acting mutations affecting the top of the cerebral system hierarchy will be selected rapidly, together with those affecting pelage, colors, and physiognomy, resulting in sub-species and races. The ever-present genetic variation in the middle layers will eventually be selected according to the changes at the top of the CNS hierarchy, resulting in new slowly emerging species-specific circuitry, while the basic layout remains constant for all mammals.

How does this scenario fit the theoretical outline of Laland et al.?

In a general way, quite well, as it postulates an extremely rapid adaptation of brain, behavior, and even morphology to changing conditions among which niche construction, protoculture, and culture are certainly important. It does not support some of the more specific predictions, however: for example, rapid evolutionary adaptation of humans might occur after changes in the environment or environment-independent niches. Also, big brains would still remain adaptive even without niche construction. Taken together, the key issue still remains that of how fast the process of genetic adaptation and speciation can occur. If it can interact dynamically with the speed of niche construction, what is conceptually more important: the evolutionary malleability of brain and behavior, or one of its derivatives, niche construction? I do not know. However, the issue of evolutionary changes in brain and behavior must be addressed, theoretically and experimentally, in order to permit less hypothetical unitary hypotheses (independent of one's sympathy for the Laland et al.'s model). We have recently shown that experimental natural selection in feralized laboratory mice changes both hippocampal connectivity and behavioral hippocampus-dependent traits after three to four generations (Wolfer et al. 1999). What would it mean if this surprising speed of genetic adaption could be extrapolated to humans?

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Selection: Units, modes, and levels

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Abstract: Niche construction theory inherits flaws from previous gene-culture coevolutionary theories. Units of cultural transmission have not yet been defined. Vertical transmission is not necessarily an overwhelmingly important part of culture. The assumption that human genetic interests and human cultural interests are in synch is a form of naive group selection.

The problem with cultural inheritance units. That culture "can be divided into recognizable subunits of transmission and inheritance" is a key assumption of the extant forms of gene-culture coevolution theory (Durham 1991, p. 420). I argue that the continued progress of cultural transmission theory will depend upon a richer elaboration of the idea of "culture" and especially the definition and description of the "transmittable 'chunks'" that Laland et al. (sect. 1.3, para. 5) rely upon. Their concept of the "phenogenotype" is not adequately described. Do they argue that, for example, Smiths (a last name, a profession, and a family lineage) are in competition, within a particular social structure, against Coopers? Perhaps they refer more to processes like the replacement of Arawaks by Caribs during the contact period. Gene-culture coevolutionary models are currently lacking a clear description of their putative units. Adding the concept of the larger amalgamation of these into a phenogenotype may be convenient for modeling purposes, but it does not yet lend itself to empirical work. I am not at all convinced that it is useful or productive to re-establish "the organism as the central unit of human evolution" Laland et al. (sect. 2.3, para. 1).

The problem with vertical transmission. I question Laland et al.'s claim that vertical transmission is overwhelmingly important (Guglielmino et al. 1995). Statistical analysis that demonstrates that language or other culturally inherited factors fit a historical model is flawed unless it explicitly deals with the fact that spatial and historical proximity are confounded (Roberts et al. 1995; Smouse & Long 1992; Smouse et al. 1986). Only the degree to which culture corresponds with genetic history, while controlling for geographic proximity, is evidence for vertical transmission. I have shown (Pocklington 1996) that the linguistic history of the populations used in the Guglielmino et al. (1985) study show independent partial correlations with both genetic and geographic distances, suggesting that for that population sample, language shift (Beeks 1995) has occurred on a substantial scale. Correlations between language and culture may represent diffusion rather than shared history. The degree to which vertical transmission is important in the long run of human cultural history is currently unknown (Rogers 1995). Laland et al. are correct in asserting that cultural characters relating to family, kinship, and social stratification may have strong vertical transmission components. Most other aspects of culture seem weakly correlated with population genetic history (Pocklington 1996).

The problem of adaptation. Cultural characters that do not follow strict patterns of vertical inheritance have an evolutionary fate that is decoupled from that of their hosts. Boyd and Richerson's (1985, p. 182) parent teacher/model shows that a trait that makes an individual more likely to be a teacher and less likely to be a parent can proliferate given that the cultural selection advantage for

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the trait and the degree of non-vertical transmission outweigh the genetic fitness cost. The less vertical the cultural transmission is, the more important cultural success is relative to biological reproduction. This situation is analogous to parasite virulence models, where horizontally transmitted elements are generally more virulent than vertically transmitted elements (Bull 1994; Bull et al. 1991; Frank 1996). Pocklington and Best (1997; Best 1998; Best & Pocklington 1999) have demonstrated that high fidelity replicating units are identifiable within cultural systems on the internet. They appear to have properties that could be referred to as additive fitness components. Investigations into their self-replication adaptations are ongoing. If small coherent cultural units have evolved transmission modes that are orthogonal to the main stream of human genetic inheritance, then the potential for gene-culture conflict of interest is an essential part of any gene-culture coevolution model. Niche construction, with its emphasis on biological fitness, and the concept of the phenogenotype should not take us a step back toward sociobiology, but forward toward a theory that can deal with the twin concepts of biological and cultural replication, both guided by adaptationist thinking. Cultural adaptation at the level of the replicating cultural trait may be an important and under-recognized force in gene-culture coevolution (Dawkins 1976, p. 203).

Summary. With attention paid to empirical data on cultural transmission and a focus on the appropriate units of selection, gene-culture coevolutionary theory with niche construction may well pave the way for the development of a new paradigm in cultural studies.

The meaning of hominid species – culture as process and product?

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Abstract: One implication of Laland, Odling-Smee & Feldman's niche construction model concerns the significance of the role of behavioural or cultural traits in comparative analysis. In this commentary it is suggested that cladistic methods already recognise this importance, and that behavioural characters may play a key role in hominid speciation and the definition of species.

Laland et al. make a general case for the importance of niche-construction in the evolutionary process and call on the human social sciences to note their model. Both suggestions will no doubt enrich the broad field of anthropology, because the niche-construction model throws into sharp relief issues concerning the definition of culture and the relationship between cultural and evolutionary change which are as old as the discipline of evolutionary biology itself. Perhaps most fundamentally, a niche-construction model in palaeoanthropology may have interesting implications for the meaning of hominid "species" and the role of behaviour in their definition.

Laland et al. suggest that phenotypic traits, or "recipient characters," may be selected in niche-constructed environments, and that these characters could be measured in closely related taxonomic units for comparative analysis and to study character evolution. It is further suggested that in humans the relationship between "genes and memes" could be studied in this way, by identifying "genetic signatures" related to a cultural meme and then using that signature to trace the history of that cultural trait across related human groups. Although the authors do not use the term, they are essentially advocating a cladistic analysis of the kind long familiar to those interested in ecology (Brooks & McLennan 1990), character evolution (Mace & Pagel 1994) and cladistic biogeography (Humphries & Parenti 1999; Nelson & Platnick 1981). Nor is their approach novel; it describes no new cultural traits; recent developments in all these fields of phylogenetics have continued to support the use of epigenetic, behavioural, or contextual data within some cladistic analyses (de Queiroz & Wimberger 1993). In one important sense, however, the niche-construction model takes one step further, in implying that the "genetic signatures" and the cultural memes are both integral and indivisible elements of the organism. This is an implication that arises as a secondary product of the model's process-orientation, but it raises the issue of whether the pattern-based morphological species concepts favoured by many palaeoanthropologists may need broadening to include characters which describe these cultural memes.

Of course, there are problems with this interpretation. Laland et al. support the view that a three-tiered hierarchical structure to the hominid information-acquiring system underlies the niche-construction capabilities of the family. They summarise these tiers as "naturally selected genes," the most phylogenetically primitive tier, "ontogenetic systems," which include open developmental systems, and language-facilitated culture defined as "a second knowledge system (within) the evolutionary process through which socially learned information is accrued, stored, and transmitted between individuals." The implication is that all three tiers can be described in terms of measurable characters and used in comparative analysis. However, much as cladists have found that for identical sets of taxa separate phylogenies based on molecular data, morphological data, and behavioural data may have different branching structures, so different processes underlying these information-acquiring tiers might be similarly reflected in comparative analysis.

This situation is demonstrated in the five evolutionary explanations for the initial speciation event resulting in the appearance of the hominid family with which Laland et al. illustrate the importance of the niche-construction model for palaeoanthropology. These scenarios can be divided into two categories; those in which the sub-populations are exposed to the same environmental conditions, and those in which they are not. In either case, the sub-populations may change the relationship they have with the environment by altering their niche-constructing behaviour, or they may not. The root of the speciation event may lie either with the hominid information-acquiring system, or the external environment, but it is the interface between the two that defines the evolutionary status of the hominid group. The implication is that genetic or morphological changes, however superficially dramatic, will only affect the status of the taxon if they are reflected in (even the most subtle) changes at this interface. This is, in other words, a process definition of species in which behaviour has centre stage.

The debate surrounding the species concept in palaeoanthropology has not been resolved, but some important issues that fuel it have been given new relevance. Concerns about changing patterns of hominid behaviour such as subsistence, social strategies, tool use, or landscape management are central not just to our description of archaeological and cultural developments, but to our understanding of the evolutionary mechanism itself. The cultural information-acquiring system may be interpreted either as an argument for a group-level unit of selection, or more conservatively as an explanation of how the group context may influence the organismal unit of selection. In either case, changes in behaviour may define hominid species as surely as changes in morphology or genes, and just as for morphology or genes, culture is both a process defining the hominid population and a product of it.

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Niche construction at the "workface" of the human behavioural sciences

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Abstract: Niche construction is a potentially important concept for the human behavioural sciences but we question how it differs from models of gene-culture coevolution and whether it can be developed in the detailed ways that will be necessary if it is going to make a significant contribution to the human behavioural sciences.

Those of us in that relatively small group of human behavioural scientists convinced of the importance of the evolutionary approach are prone to frustration with our less evolutionarily committed colleagues. The non-evolutionary stance of most social science – the Standard Social Science Model of Tooby & Cosmides (1992) – is so entrenched that it is often difficult to see what will shift it. A cataclysmic shaking of its foundations was promised by sociobiology (Wilson 1975), but never quite delivered. More recently, evolutionary psychology (Barkow et al. 1992) has opened up some cracks through which the shoots of a thoroughgoing evolutionary approach might be able to grow.

Against this background, niche construction is a potentially important "node" around which the evolutionary modelling of the complexities and intricacies of human behaviour, cognition, and social systems could take place. However, we have two reservations about niche construction. One is whether the concept really offers anything radically different from models of gene-culture coevolution. The other is whether it can be developed in the detailed ways that will be necessary if it is going to make a significant contribution to the human behavioural sciences.

The concept highlights the fact that the behaviour of organisms can modify their environments in ways that alter the selection pressures operating on them and their descendants – the "feedback from niche construction." This is a useful reminder that selection pressures do not stem solely from sources independent of the organism, such as climatic changes or the activities of other species. It also directs us to think of species as being in true dynamic interaction with their environmental selection pressures. But it does not force us into any radical rethink of the evolutionary process.

To take one of the animal examples given by Laland et al., it is doubtless true that contemporary earthworms live in worlds that have been partly niche-constructed by generations of their burrowing ancestors changing the construction and chemistry of soils. But how much does it really add to our understanding of the evolutionary process in general, or earthworm evolution in particular, to know that "other earthworm phenotypes, such as epidermis structure or the amount of mucus secreted, have probably coevolved with such niche-constructing behaviour" (sect. 1.1, para. 9)? The processes underlying the evolution of these phenotypes are not fundamentally different from those which would have been involved had the selection pressures stemmed purely from independent changes in soils.

Of course, the real thrust of the target article is the human case, and the obvious fact that human niche construction is much more extensive and more complex than that of animals could mean that the concept has more potential in this context. Even here, however, the niche construction model so far promises more than it delivers. It is significant that the human examples with which Laland et al. seek to illustrate their model in section 2 centre, for the most part, around some fairly general (although important) issues in hominid and human evolution. These are precisely the sort of issues the model is best equipped to tackle. But it does mean that the initial application of the niche construction model to the human behavioural sciences is taking place at a relatively abstract level. Granted, the building of abstract models for understanding the relationships between biological evolution and cultural processes is an important part of the process of the accretion of evolutionary ideas in human behavioural science. But abstract models alone will almost certainly not be enough to entice our human behavioural science colleagues out from behind the barricades of traditional social and cultural theory. What will be needed, in addition, will be some indications as to how such models can be extended to shed new light on the specifics of behaviour, cognition and society. In the long run, the success of the niche construction model (or of any other evolutionary model claiming relevance to the human behavioural sciences) will be assessed in terms of its ability to offer new insights into human psychological and social traits that exist are relatively specific levels. Can the model help elucidate, for example, the psychology of human mate preferences (Buss 1994; [see also Buss: "Sex Differences in Human Mate Preferences" *BBS* 12(1) 1989; and Kenrick & Keefe: "Age Preferences in Mates Reflect Sex Differences in Human Reproductive Strategies" *BBS* 15(1) 1992]) or the evolution of the brain mechanisms underlying the recognition and reproduction of human actions (Carey et al. 1997)? Cognitive scientists, developmental psychologists, sociologists, social anthropologists and the like will need convincing that there is something for them in the niche construction model at the detailed "workface" level at which they go about their daily business.

The hard part for evolutionary theorists is getting their theories to the stage where human behavioural scientists become sufficiently convinced of the importance of the evolutionary approach that they start applying evolutionary models for themselves, developing them and testing their boundaries. We must show them that embarking on this endeavour is not only possible but essential, and that it can take us way beyond the confines of the standard social science model, with its old sterile dichotomies of biology versus culture and genes versus environment and the spectre of genetic determinism. Perhaps we might eventually reach a critical stage where the development of evolutionary models in the human behavioural sciences picks up enough momentum to steamroller the standard social science model once and for all. How much the niche construction model has to contribute to this process remains to be seen.

The compound interest effect: Why cultural evolution is not niche construction

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Abstract: Laland et al. rightly observe that the pressures affecting the evolution of a trait include the previous effects the trait has had on the environment. Ignoring this would be like ignoring the effect of compound interest: a distortion, not a simplification. However, cultural evolution is not niche construction. In niche construction one mechanism has effects over multiple paths. Cultural evolution involves the effects of several mechanisms.

Laland, Odling-Smee & Feldman are right in pointing out the importance of niche construction. The standard model of evolution, as they describe it in Figure 1a, is a simplification of the actual ways in which genes affect evolution. This simplification is like the simplification committed when one ignores the effect of compounding interest. However, in attempting to assimilate cultural evolution and niche construction they are conflating three distinct evolutionary mechanisms.

The interest paid (or charged) on a savings account (or a loan) can be simple or compound. Simple interest is paid on the principal alone. Thus a $100 savings account which pays 5% simple interest every year, will generate $5 of interest each year. If the in-

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terest is compounded, then the interest from one year becomes part of the basis for the interest calculation for the next. Thus the same $100 at 5% interest, compounded, will pay $5 the first year, and then 5% of $105 the second year, and so on. Small difference for one year, perhaps, but after 20 years, the account at simple interest is worth $200, while at compound interest $265. Something similar is true of the effects of (genetically determined) behavior. Regular patterns of behavior affect the environment, changing the environment in small ways so that future members of a species face altered selection pressures. The difference in these selection pressures might not be much between two consecutive generations, but over time the differences grow. Thus, it would be a mistake to think that there are external, environmental, selection pressures, and internal, genetic, responses to those selection pressures, and never the twain shall meet. Instead, we would have a more complete understanding of evolution were we to acknowledge that future genotypes are determined by present genotypes in part through genetic inheritance and in part through the effects that genotype has on the future environment. Call this the compound interest effect.

For example, burrowing animals affect the evolutionary pressures felt by their descendants in two ways. Their descendants inherit the genes for burrowing, and they inherit the niche of the burrow. These legacies are both products of the same initial cause: the genes for burrowing. They cause the burrowing behavior, and the burrowing behavior creates the niche, which exerts future selective pressure. This is the compound interest effect: the same mechanism compounds its effects by operating through more than one channel. The compound interest effect occurs when the genes of the present generation effect the genes of future generations by means of both standard genetic inheritance and the indirect effect those genes have on the environment of the future generations. Thus the compound interest effect is merely an important variant of the standard picture of evolution given in Figure 1a: the transmission of traits is still genetic, the difference being that now we recognize that the genes of the current generation affect both the genes and the environment of the future generation. Niche construction is a paradigm example of the compound interest effect. Cultural evolution, on the other hand, involves more than just the effects of genes through more than one pathway. In their claim that cultural evolution is a subspecies of niche construction, Laland et al. are ignoring important differences between cultural evolution and niche construction.

"Cultural evolution" refers to one of two disparate phenomena. It can refer to the effects that culture has on evolution, or to the way culture itself evolves. For example, the increased presence of the gene for sickle-cell anemia in the Kwa-speaking yam cultivators in West Africa is an evolutionary effect of a cultural behavior. On the other hand, that they cultivate yams is itself a culturally transmitted behavior. Laland et al. (sect. 1.3, para. 5) label this transmission of knowledge (and presumably attitudes, strategies, etc.) within a culture, "cultural inheritance." In order to distinguish these two phenomena I will save the label "cultural evolution" for the former, and use "cultural inheritance" to refer to the latter.

Is cultural inheritance a species of the same phenomenon as niche construction? If this were so, either cultural inheritance would be a product of the same mechanisms that drive niche construction, or cultural inheritance would be analogous to niche construction. The first option is notably controversial, for this would require our genes to be significant determinants of human culture as well as of the behaviors that result in the cultural transmission of knowledge. Perhaps genes do have these effects, but Laland et al. have not argued that they do. The second option is less controversial, but it is equally less applicable. For cultural inheritance to be analogous to niche construction would require that the same mechanism that determines that some ideas spread throughout the culture also determines the effects of those ideas on future cultures. But we generally think that the effect the ideas have on the environment is a consequence of their content, while the spread of the ideas is a consequence of many factors, including their utility, the force with which they are promulgated, and so on.

Is cultural evolution a form of niche construction? The effect of yam cultivation by the Kwa-speakers of West Africa was to alter their environment, their niche, and this change in environment had the genetic consequence of increasing the frequency of the gene for sickle cell anemia. However, unless Laland et al. are prepared to argue that the Kwa-speakers cultivated yams because of some genetic disposition to do so, there is a significant disanalogy between cultural evolution and niche construction. When the burrowing animal changes its environment, and thus the selection pressure affecting it, as a result of living in burrows, this change in the environment is a direct consequence of the way its genes influence its behavior. When the Kwa-speakers of West Africa change their environment, and thus the selection pressures affecting them, as a result of cultivating yams, this change is a direct consequence of their culture and not of their genes. Cultural evolution is a much more complex phenomena than niche construction; niche construction is merely a demonstration of the compound interest effect, whereas cultural evolution is a result of at least two different forces: the effects on the genome of the altered environment, and cultural inheritance.

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Human creativity, cultural evolution, and niche construction

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Abstract: Cultural evolution may be even more prolific in the generation of new forms than is biological evolution – especially when it takes the form of creative genius. Yet evolutionary theories have tended to overlook the factors that might select for outstanding individual creativity. A recent dual-inheritance theory is outlined and then integrated with the niche-construction theory of Laland et al.

The two most creative processes on this planet are biological and cultural evolution. The former has generated all the diverse life forms, both extant and extinct; the latter has produced the tremendous diversity of human cultures, including the wealth of adaptations, artifacts, and symbols that constitute technology, science, art, religion, and politics. It has even been argued that of the two creative forces, cultural evolution has been the more prolific in the production of innovations. According to patent statistics alone it is clear that human inventions are as diverse as all the species that currently inhabit the earth (Basalla 1988). When to this figure is added all inventions, artistic products, scientific discoveries, religious creeds, philosophical positions, languages and dialects, fashions and customs, political, social, and economic systems – the sum of distinct cultural innovations may well surpass all species that have ever populated the earth (Simonton 1999). Even more remarkable is another fact: Once societies evolve to a sufficient level of complexity, certain individuals emerge who specialize in the generation of new ideas. In the extreme form, these persons may be styled "creative geniuses" and thus enjoy celebrity, such as Copernicus, Descartes, Shakespeare, Beethoven, and Michelangelo. The ability of these creators to produce new ideas, or "memes" (Dawkins 1986), can be prodigious. For example, Thomas Edison alone held well over a thousand patents, a figure approximately equal to one quarter of the total number of extant species of mammals. And the difference between a phonograph and a light bulb may be as great as that between a whale and a bat

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(see Simonton 1999 for further discussion of this comparison).

Any comprehensive evolutionary theory should explain the origins of creative genius. Yet this phenomenon presents special theoretical difficulties. Although creativity may be good for the society as a whole, outstanding creators tend to have characteristics that may be maladaptive to themselves, both culturally and biologically (for literature reviews, see Eysenck 1995; Simonton 1999). For instance, creative ability is associated with extreme independence, nonconformity, and introversion, which would undermine the individual's adaptation to social norms and expectations. Creativity also correlates with certain tendencies toward cognitive, behavioral, and emotional disorders, including outright psychopathology that would seem to vitiate individual adaptive fitness in a biological sense. In fact, exceptional creative achievers are most likely to come from family pedigrees that display elevated rates of various psychological disorders. So, what are the selective forces that would support the emergence of such high-level creativity?

Some evolutionary theorists have argued that biological evolution alone could account for the appearance of human creativity. For example, Charles Darwin thought that some forms of human creativity emerged through sexual selection, an idea that has been developed by recent theorists (e.g., Miller 1997; 1998). Even characteristics that have maladaptive side effects might still be so favored if there were compensating advantages, in a manner analogous to sickle-cell anemia (e.g., Hammer & Zubin 1968; Huxley et al. 1964). On the other hand, it may be that a complete explanation will have to incorporate cultural evolution, perhaps operating in conjunction with biological evolution, as in co-evolutionary or dual-inheritance theories (e.g., Boyd & Richerson 1985; Lumsden & Wilson 1981). Yet, unfortunately, the latter theoretical developments have tended to ignore the question of human creativity (for a partial exception, see Findlay & Lumsden 1988).

I have recently tried to remedy this deficiency in a book appropriately entitled *Origins of genius: Darwinian perspectives on creativity* (Simonton 1999). The theory begins with the assumption that the creative process is fundamentally Darwinian, as argued in Campbell's (1960) blind-variation-and-selective-retention model of creativity and as implemented in genetic algorithms and programming (Goldberg 1989; Koza 1992). Creativity thus constitutes a "secondary Darwinian mechanism" analogous to selectionist models of antibody formation (Söderqvist 1994) and neurological development (Edelman 1987). The theory then addresses the complex issue of the various cognitive, dispositional, developmental, and social factors responsible for the substantial individual differences in the ability to engage in this Darwinian process (see also Eysenck 1995; Simonton, in press). Once these connections are established, the theory is free to examine the possible selection pressures that may encourage the emergence of these "Darwinian minds." Without denying the potential impact of biological evolution, including sexual selection, the theory outlines a model based on cultural evolution, which in turn exerts selective pressures on biological evolution.

At this point my theory joins the niche-construction theory of Laland et al. Among the selection pressures I discuss is the ever more urgent need for individuals and cultures to adapt to new niches. This necessity is accelerated by several factors, including (a) excessive niche exploitation that leads to resource depletion (and hence the pressure to identify new niches), (b) population growth that stimulates the development of internal niches (i.e., new social roles, as in Spencerian evolution), and (c) strong intergroup competition that instills a dynamic disequilibrium (as in preditor-prey or parasite-host co-evolution). The upshot is augmented selective pressure in favor of characteristics that enable individuals to engage in the Darwinian recombination of memes (cf. the "red queen" basis for sexual recombination in Ridley 1993). Although niche construction is not explicitly mentioned in this argument, this factor would be likely to participate in this procreativity selection process in at least two ways. First, niche construction usually presupposes the capacity to construct new environments, such as the invention of new forms of food, shelter, and clothing. This capacity entails human creativity. Second, niche construction changes the environment in various unpredicted ways so that additional human adaptations may be required in the future, again intensifying the need for an ample supply of persons in the population who can generate the Darwinian recombinations of memes.

Laland et al. are accordingly to be congratulated for an intriguing theory that already renders my brand-new theoretical model obsolete!

An evolutionary interpretation of intelligence, creativity, and wisdom: A link between the evolution of organisms and the evolution of ideas

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Abstract: I show that there is a link between the evolution of organisms and the evolution of ideas. In particular, if conformity is selected for, then mechanisms are needed so that "mutations" of ideas can occur. Creativity acts as a counter-force to conventional intelligence, so that ideas can develop that do not just elaborate existing paradigms, but oppose these paradigms. Sometimes oppositional ideas go too far, however, and wisdom acts as a force to bring the old and the new together. The dialectic thus integrates intelligence, creativity, and wisdom, with intelligence serving as thesis, creativity as antithesis, and wisdom as synthesis.

Suppose it really is the case, as Boyd and Richerson (1985) and now Laland, Odling-Smee & Feldman suggest, that selection works at a cultural level, with cultural traits at the group level being selected. The result, as Laland et al. indicate, is that those who conform – those who do "as the Romans do" – will be at a selective advantage. They are more likely to be accepted by the group and less likely to be ignored, punished, or even expelled from the group than those who choose not to conform.

If conformity is selected for, the long-term prospects of a culture are dubious. In the long term, organisms will be in terrible trouble as a result of stagnation, unless cultural evolution allows for mutations in the same way that natural evolution does.

The dialectic. I suggest that there is a mechanism that allows "mutant" thoughts to exist and even at times to permeate a culture. This mechanism begins with the dialectic. Hegel (1931) proposed that, over time, ideas evolve in a dialectical fashion. First, a thesis is proposed. This thesis, analogous to a scientific paradigm (Kuhn 1970), serves as a foundation for a field – for scientists, artists, writers, or whoever works within the assumptions and world-view of the existing paradigm. After a while, one person – or more – proposes an antithesis, which rejects the ongoing paradigm. The initial reaction to this rejection is often negative (Sternberg & Lubart 1995), although as time goes on, workers may be forced to recognize that the assumptions and world-view of the original thesis are no longer viable – that this world-view is imploding. Often, however, the antithesis goes too far in the rejection of old ideas. Old ideas that were initially seen as useless are eventually seen to have some value and to have made some contribution. Thus, a synthesis is reached, whereby the new is successfully integrated with the old, and this synthesis ultimately becomes the new thesis.

Relation of the dialectic to intelligence, creativity, and wisdom. Intelligence, as traditionally defined, serves as a basis for successful adaptation to the environment created by existing world-views (see Sternberg & Kaufman, in press). Indeed, intelligence is usually defined as the ability to adapt to the environment

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(see Sternberg & Detterman 1986). But if the only thing people did was to adapt to existing ideational environments, cultural evolution would stagnate. The culture would become wholly self-replicating and it would stop evolving. As proposed in science-fiction novels of such stagnant cultures, however (e.g., Lowry 1993), there is a solution.

Every once in a while, ideational mutants come along, creative individuals who are consistently willing to "defy the crowd" (Sternberg & Lubart 1995). These individuals reject the current thesis or theses as embodied in the existing paradigm (Sternberg 1999). They suggest ideas that are both novel and high in quality, thereby providing the antithesis to the currently accepted view. Their creativity often comes at a cost to themselves and to those around them.

Creative people often go too far in the rejection of existing paradigms, however. In their desire to overthrow the existing order, they may exaggerate the flaws in that order. Wisdom, which requires a delicate balancing of ideas and interests (Sternberg 1998), then prevails, and one or more wise individuals see how to synthesize the old order of ideas with the new order that has made (or is currently making) headway.

My suggestion, then, concerns both how intelligence, creativity, and wisdom relate to each other, and how the evolution of organisms and of ideas relate to one another. Intelligence, as traditionally defined, reflects the organism's ability to adapt to the existing environment. Very intelligent people adapt better, and work the ideational system to their own advantage. They either replicate existing ideas or increment these ideas in a forward direction. They advance the current thesis. Very creative people often do not adapt so well and often work to overturn the existing ideational system in favor of a new one. They advance a new antithesis. Very wise people attempt to integrate the new with the old, and work to establish an ideational system that synthesizes the new with the old. They advance a synthesis that integrates these two sets of ideas. Thus, the evolution of ideas, like the evolution of organisms, should never stagnate for an indefinite period of time.

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Niche construction and group selection

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Abstract: The antipathy toward group selection expressed in the target article is puzzling because Laland et al.'s ideas dovetail neatly with modern group selection theory.

Laland et al. deserve enormous credit for requiring us all to think in more dynamic terms about the relationship between an organism and its environment. Like "stimulus" and "response" in psychology, the concepts, "organism" and "environment" are more complex and mutually entangled than they appear. A response is required to pick a stimulus out of a stream of events in an animal's world, and a stimulus is required to pick a response out of the stream of behaviors emitted by an animal. Similarly, we cannot designate an environment except that it is an environment for some organism or designate an organism except that it moves against the background of some set of circumstances called the environment. Not only are the concepts, organism and environment, necessarily inter-defined, they are also not mutually bounded in quite the way their usage would suggest.

Just as part of what constitutes the "stimulus" for a "response" is anticipation of and feedback from that response, so part of what constitutes the environment consists of extensions of the organism itself into the environment. Thus, these authors have helped us to see that just as we have seen limits to what an atomistic behaviorism can be expected to do for psychology, so inevitably we must prepare for the day when we reach the limits of what an atomistic population genetics can do for biology.

One way to understand niche construction is to say that selection can act on larger temporal units than the lifetimes of single organisms. Put this way, their point seems to supplement one made here by Wilson and Sober recently (1994; 1998; see also Sober & Wilson 1998; Thompson 1998a) to the effect that selection can act on organizational units larger than individual organisms. Because I tend to see the present target article as part of a newfangled dynamic biology that has natural selection acting in broader time spans and organizational levels (e.g., Michod 1999), I was startled to see these authors reject group selection in what seemed an uncharacteristically oldfangled way. This passage is startling because the niche-construction activities of organisms seem just the sort of phenomena that contemporary group selection theories are ideally suited to explain: that is, a situation in which the benefit to the group of individual activity is a function of the proportion of individuals in the group that perform it. Under these circumstances niche construction would be selected for, even if it exacted some cost from niche constructors, because groups with many niche constructors would make a disproportionately large contribution to the next generation. This favorable selection could go forward, even though niche constructors were being selected against within each and every group.

Laland et al.'s misgivings about genetic group selection seem to arise from three sources: concerns about variation within and among groups, concerns about group sizes, and concerns about the relative efficacy of group selection vis-à-vis kin selection and reciprocal altruism. The authors are correct to worry about within- and among-group variation, but incorrect to worry so *much* about it. The difficulty to be gotten around is the fact that some group members benefit "unfairly" from the niche construction activities of other group members. But Wilson (1980) has shown that so long as group productivity is a non-linear positive function of the number of individuals engaged in niche construction, random variation between and within groups can generate group selection that is sufficiently strong to explain this sort of inequity within groups.

Similarly overwrought are Laland et al.'s worries about group size. Although most modern cultures are probably too large and diffuse to promote much group selection of the kind that Wilson and Sober suggest, this fact is irrelevant. As evolutionary psychologists are endlessly fond of pointing out (Barkow et al. 1992), the relevant selection pressures are not modern ones but those that were effective during the Pleistocene, when human groups were much smaller and more isolated than they are now.

Finally, Laland et al. appear to be influenced by the old notion that reciprocity and kin selection are alternatives to group selection rather than mechanisms that work in concert with it. Kin selection works because cooperating kin-groups are more productive than non-cooperating ones. Reciprocity works because groups of reciprocators are more productive than groups of non-reciprocators. Neither mechanism works unless the group – the whole – is greater than the sum of its parts. This "greater-than-the-sum-of-its-parts-ness" defines group selection and is a starting condition for any explanation of cooperation.

The absurdity of seeing kin-selection, reciprocal altruism, and group selection as antagonists is made clear by thinking precisely

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about the metaphor embodied in natural selection and what it means to frame shift that metaphor to a new level of organization (Thompson 1998b; submitted). When a pigeon fancier selects a pigeon for the quality of its plumage, that pigeon is chosen to propagate in the expectation that its offspring will also have high quality plumage. This outcome is assured by genetic mechanisms. Similarly, when nature selects for the coherence and effectiveness of a group, the group is chosen to propagate "in the expectation that" the group's offspring groups will also be more coherent and effective.

The three mechanisms that are often thought to compete with one another as selection mechanisms, kin selection, reciprocal altruism, and trait-group selection are better thought of as genetic mechanisms that connect the success of groups in one generation with proliferation of such groups in the next generation. Kin selection works because if the offspring of one mother form an effective kin group, then the offspring of these offspring are likely to form effective kin-groups as well. Reciprocal altruism works because if pairs of reciprocating altruists form effective groups, then the offspring of these reciprocating altruists will be more likely to form effective reciprocating groups as well. Trait group selection works because if the effectiveness of groups is proportional to the number of group-promoting individuals in the group, then to the extent that an offspring group is an offspring of an effective group, it too will have more group promoting individuals and be more effective. In all three mechanisms, individuals are not the objects of selection but the vectors that carry the group forming tendencies between generations of groups (Sober 1984). The individuals are analogous to the genes in an individual selection model. Just as in individual selection, selection is for individual traits and genes carry the traits between generations of individuals, so in group selection, selection is for group traits and individuals carry these traits between generations of groups.

Stating group selection in this form should make clear just how compatible it is with the notion of niche construction, because group selection stresses the lineal descent of groups through time and niche construction stresses the lineal descent of the group's environment through time.

Adaptation and intracultural variation

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Abstract: Inclusion of cultural variables in the study of human evolution is essential but introduces problems of vagueness, nonspecificity, and overgeneralization. Recognition of intracultural variation and conflict, and inclusion of ontogenetic processes such as individual learning are antidotal.

Laland et al.'s attempt to integrate the study of biological and cultural evolution with the concept of niche construction is heuristic. Particularly interesting were the discussions of the role of horizontal and vertical information transmission in cultural evolution (sect. 2.1.3) and how niche construction can help to explain punctuated macroevolutionary trends in the fossil record (sect. 2.1.2). Notable also is their refinement of the group-selection explanation of human altruism. Without doubt, niche construction and other cultural variables are relevant to the solution of many questions in human evolution. There are, however, at least two problems that cultural analyses typically face.

(1) "Culture" and cultural traits (e.g., socialization, social solidarity, sex role, group cohesion, values) are frequently reified and turned into causes. To be empirically meaningful, such traits must be specified and, ideally, quantified. Otherwise, they tend to function as unfalsifiable, omnibus explanations (Nagel 1961; Spiro 1961).

(2) Treating culturally transmitted traits as adaptive (sect. 1.3), and populations as homogeneous for these traits can obscure important variation and conflict. Behavior that is adaptive for one group or class of individuals may be detrimental to other groups and classes. Conflicts between bloodlines, social classes, and the sexes come to mind (Symons 1979). Sexual dimorphism in human reproductive strategies, for example, leads to strategic interference and mental mechanisms that function to reduce interference (Buss 1989; 1995; Townsend 1998).

Studies that used different instruments and sampling methods revealed that many contemporary women express extremely permissive attitudes and engage in multiple casual sexual relations (Townsend 1995; 1998; Townsend et al. 1995). Nevertheless, even the most permissive women tend to experience negative emotional reactions to low-investment copulation (anger, remorse, feeling used), and increasing experience with casual relations does not seem to mitigate these reactions and may exacerbate them. Such feelings cause a sizable proportion of permissive women to adopt a more conservative sexual pattern that includes higher levels of investment and denial of sexual access when investment is inadequate.

In contrast, for men, such thoughts and feelings correlated negatively with number of casual partners. Furthermore, women with permissive attitudes do not always contracept effectively (in part, because sexual emotion and passion were designed by natural selection to produce pregnancy rather than prudent contraception). Unwanted pregnancies often lead to abortion or offspring being given up for adoption. Even women who accept these courses as logical tend to experience remorse, guilt, and depression (Gilligan 1982) and may suffer a reduction of fitness (in addition to that potentiated by the medical risks of abortion). These findings suggest that culturally transmitted traits such as sexual attitudes may be adaptive for some classes of individuals and maladaptive for others.

A related problem exists in determining the degree to which a cultural trait is adaptive and the contexts in which it is adaptive. As the authors point out (sect. 2.3.2), in contemporary societies, cultural traits can be largely divorced from local ecological pressures, and this may also have been true of our hominid ancestors. Given that most contemporary populations live in environments that are radically different from ancestral environments, for some questions it may be more valid to focus adaptive analysis on the mental/emotional mechanisms that guide behavior, rather than behavioral phenotypes and products themselves (Symons 1989).

Laland et al. wisely anticipated some of these problems when they wrote (sect. 1.3) that a comprehensive treatment of the gene-culture relationship requires inclusion of all three sets of information-acquisition processes: genetic, ontogenetic, and cultural (which also includes intermediate ontogenetic processes such as individual learning). This is an interesting target article that should shape future theory and research.

Niche construction: A pervasive force in evolution?

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Abstract: Industrial melanism, according to the traditional explanation, amounts to niche construction since it involves changes in predation pressure. Indeed, it would be difficult to imagine selection without niche construction. This cannot be what Laland, Odling-Smee & Feldman mean. They offer convincing examples, but they should provide a better definition of "niche construction" to indicate how their view supplements traditional evolutionary biology.

Laland, Odling-Smee & Feldman show convincingly that traditional evolutionary theory should be expanded to account for

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niche construction. They provide compelling examples, and I agree with their overall outline. My comment is a call for further clarification rather than a criticism.

First and foremost, I would welcome a more precise definition of niche construction. Laland et al. offer the following definition. "Niche construction refers to the activities, choices, and metabolic processes of organisms, through which they define, choose, modify, and partly create their own niches" (sect. 1.1, para. 1). In a footnote they add that "construction" refers to a physical modification of the environment and not to the perceptual processes responsible for constructing a mental representation of the world from sensory inputs. The first part of the footnote, however, is at odds with the thesis that selection from niche construction may initiate new evolutionary episodes in an unchanging external environment (sect. 1.1, para. 14). Further confusion arises from apparently interchangeable uses of "niche," "(external, physical) environment," "selective environment," and "habitat" in the target article. We are told that niche construction causes changes in selection pressure. I assume that this implies a change in the selective environment, not necessarily a change in the external environment or the habitat.

Consider the classic example of industrial melanism, which is explained by traditional accounts of selection. If dark morphs replace light morphs in butterfly populations exposed to industrial pollution, predation pressure decreases due to camouflage in the butterflies. This need not amount to a change in the external environment or habitat. It does involve a change in the niche and in the selective environment. The predators remain the same, but the changes in morph color result in a different predation pressure. So, barring the footnote contradicted by the comment in section 1.1, para. 14, we should regard this as an example of niche construction. Indeed, all traditional examples of natural selection should count as examples of niche construction because they involve changed niches and changed selective environments. Surely this cannot be what Laland et al. have in mind.

Also confusing are suggestions to the effect that selection through niche construction fills explanatory gaps in traditional accounts. It is unclear how many gaps are filled by the niche construction account. I consider two examples.

First, in section 1.3, para. 7, Laland et al. argue that niche construction often involves social learning and cultural inheritance. They describe extensively the effects of learning and culture, but they do not specify which effects count as niche construction. They do state that "we have now come some way from the simple, sociobiological descriptions of gene-culture interactions. . . . We have brought together two different bodies of theory, gene-culture coevolution and niche construction." This presupposes that gene-culture coevolution cannot explain all evolutionary processes involving social learning and cultural inheritance. Niche construction allegedly fills this explanatory gap in sociobiology, but the nature of the gap is not described. To understand the surplus value of niche construction, we need a definition of "niche construction" that improves on the one provided by Laland et al.

Second, Laland et al. note that the traditional theories of kin selection and reciprocity cannot explain all instances of cooperation (mutualism) and apparent altruism, and they suggest that niche construction fills the explanatory gap (sect. 2.2, para. 1). "Our evolutionary framework indicates, however, that the suite of processes that may be regarded as plausible evolutionary explanations for human cooperation is considerably larger than kin selection and reciprocity alone." Likewise for cooperation in animals. This is clarified by the suggestion that organisms should cooperate with other organisms, if the other organisms have niche-constructing outputs that generate resources for the cooperator which, in fitness terms, exceed the costs of cooperation. Laland et al. mention a survey by Connor in support of this, without giving particular examples. Let us consider one of the examples (Connor 1995a), foraging in the colonial cliff swallow *Hirundo pyrrhonota*. The swallows forage on insects in the air. If they come across a swarm of insects, they emit calls alerting conspecifics that food has been located. On a superficial interpretation, the calls represent altruism, because the birds would do better if they kept the insects for themselves. However, they actually benefit from their behavior because it is difficult for individual swallows to track insect swarms. Should we regard this as an example of niche construction? The clarification above does not help us answer this question because it is unclear whether the swallows can be said to "generate" resources for conspecifics.

More important, the elusiveness of the definition of "niche construction" is unhelpful. If changes in the external environment are a defining criterion, the behavior of the swallows is not niche construction. If changes in the selective environment are a criterion, we are dealing with niche construction, but as I argued, this criterion would have the awkward implication that all cases of natural selection involve niche construction. I would suggest that some but not all mutualisms involve niche construction. To distinguish between the categories, we need a more precise definition of "niche construction."

The challenge of understanding complexity

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Abstract: Those who emphasize complexity must show how it can be studied productively. Laland et al.'s target article partially succeeds but at times gets lost in a sea of possibilities. I discuss the challenge of understanding complexity, especially with respect to multilevel evolution.

I have a love-hate relationship with scientific arguments that celebrate complexity. On the one hand, they are exactly right. The world *is* a complex place, which simple explanations ignore to their peril. On the other hand, emphasizing complexity often results in a combinatorial explosion of possibilities that paralyzes scientific inquiry. It is possible to read a holistic paper and agree with every single point, yet feel no more enlightened at the end than at the beginning.

Laland, Odling-Smee & Feldman, following Lewontin (1983), are surely right that a feedback process exists between organisms and their environments, which can be intensified by cultural processes. The reason that Lewontin's idea (and its precursors) has remained largely dormant is not because it is wrong but because it is hard to know what do to with it. At least for me, Laland et al.'s revival is effective at stressing the rightness of many specific points, but less successful at demonstrating how they can be combined into an effective research program. I do not wish to appear too critical, however, because I am in the same situation. Those of us who appreciate complexity are like climbers at the base of a formidable mountain, trying to plan a route to the summit. I offer four suggestions in a constructive spirit.

1. *Simple explanations sometimes suffice.* Many of Laland et al.'s examples are already well understood from simpler perspectives. It is true that spider webs, mammal burrows, and termite mounds had to exist in their basic form before subsequent adaptations could evolve in the structures and the organisms inhabiting the structures. However, what does emphasizing the evolutionary feedback between organism and environment add to our understanding of these adaptations? For many purposes, we can simply ask how burrow-dwelling animals evolve in their burrow environments. In general, if the macroevolutionary feedback process is sufficiently slow, the environment can be treated as a constant for short-term evolutionary change.

2. *Partitioning complex subjects into simple components.* My own mountain of complexity is multilevel selection theory (MLS) (Sober & Wilson 1998; Wilson 1998; Wilson & Kniffin 1999; Wilson & Sober 1994; Wilson et al. 1999), which Laland et al. discuss in the process of illustrating their own framework (sect. 2.2). I am

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disappointed in their treatment for reasons that bear on the general problem of understanding complexity in addition to the details of MLS theory. In their example involving organisms O_1 and O_2, Laland et al. appear to have forgotten that natural selection is based on relative fitness (Williams 1966). What is the point of calculating the net gain for O_1 without comparing it to the net gain of alternative types that do not cooperate? Determining what evolves in this example requires far more information than provided – a sad comment for a paper that is supposed to appreciate complexity and show how to deal with it. We need to know the degree to which the benefits of cooperation are shared, the presence of groups, how the types are distributed into groups, and other details of group formation and dissolution. MLS theory attempts to understand this complex process by breaking it into simpler components; a within-group component based on relative fitness within groups and a between-group component based on the relative fitness of groups in the global population. MLS models are frequently used to study the evolution of altruistic traits, which by definition are selected against within groups and favored at the group level. Some forms of altruism require extreme self-sacrifice but other forms can create powerful group-level benefits at only minor within-group cost, requiring correspondingly weak group selection to evolve. In addition, complex interactions within groups can produce multiple stable equilibria, allowing group selection to proceed without any opposing within-group selection (Boyd & Richerson 1990). The models of Boyd and Richerson are examples of MLS theory, not alternatives to it, as Laland et al. seem to imply. Population structure is not a fixed part of the environment but itself can evolve, sometimes concentrating natural selection at upper levels of the biological hierarchy, resulting in a "major transition of life" (Maynard Smith & Szathmary 1995). All of these complex processes can occur in nonhuman species but can be greatly amplified by culture. Properly understood, MLS theory illustrates many of the general points that LOF are trying to establish and offers a disciplined way of scaling this particular mountain of complexity. It is therefore frustrating for Laland et al. to dismiss the framework so casually with underspecified models of their own.

3. *The need for detailed empirical studies.* When theory outlines a parameter space that is too large to explore in its entirety, empirical research is required to discover the regions of the parameter space that are occupied by real-world biological and cultural systems. The debate about adaptationism in evolutionary biology would be futile were it not for extensive research programs that measure natural selection and its constraints in guppies and many other species (Endler 1986; 1995). Some of Laland et al.'s strongest sections are based on the empirical reviews of Durham (1991). Other outstanding examples not cited by Laland et al. are Kelly's (1985) analysis of the Nuer conquest (discussed from an evolutionary perspective by Sober & Wilson 1998), MacDonald's (1994) analysis of Judaism as a group evolutionary strategy, and MacDonald's (1995) analysis of the origin and spread of socially imposed monogamy in Europe.

Many kinds of empirical research on humans are difficult or impossible, either for ethical reasons or because the relevant information cannot be obtained. However, other kinds of research are not only possible but vastly easier for humans than for nonhuman species. In particular, a fossil record of cultural change exists for our species that puts the biological fossil record to shame. The psychological mechanisms that underpin cultural change are also wide open for empirical research (Fiske et al. 1998). Entire disciplines in the social sciences and humanities are devoted to these subjects and the quality of science and scholarship is often excellent. All of this is data that awaits analysis from Laland et al.'s conceptual perspective. My own efforts in this direction involve the study of religious belief systems during the Reformation, centering on Calvinism. The historical record is detailed enough to reconstruct the origin, structure, internal evolution, interactions, and ultimate fate of the many varieties of religious faith that existed during the period. For Laland et al.'s agenda to move beyond the theoretical stage, empirical research programs in cultural evolution must become as ambitious as research in biological evolution.

4. *Adaptationism.* Evolutionists are often criticized (often by other evolutionists) for placing too much emphasis on the concept of adaptation (Gould & Lewontin 1979). The importance of adaption in nature is an empirical issue but there is another reason why adaptation should have an important status in evolutionary thought. Often it is relatively simple to predict how an organism should be structured to survive and reproduce in its environment, at least compared to predicting the many factors that might prevent these structures from evolving by natural selection. Imagining what a well-adapted organism would look like therefore serves as a first guess that is expected to be wrong to a greater or lesser degree. If the predictions are completely wrong, then it is back to the drawing board. If the predictions are partially confirmed, then the deviations can actually help to identify the constraining factors emphasized by critics of adaptationism. When seen as a method of inquiry rather than a statement about nature, the adaptationist program (a term used as a pejorative by Gould & Lewontin) withstands most of the cricisms levied against it. It is not the only method of studying evolution, but it is a powerful method.

Can the adaptationist program be employed at the level of human cultures? To state the conjecture boldly, could a human community organized by a cultural belief system such as Calvinism be regarded as a superorganism, complete with an intricate "social physiology" (a term used by Seeley 1995 to describe the adaptive organization of insect colonies)? Do most details of a cultural belief system have an organ-like function? This kind of group-level functionalism was common among the founding fathers of the social sciences but fell into disrepute, largely for the same reason that adaptationist hypotheses are branded as "Just-so" stories within evolutionary biology. Of course, many evolutionary biologists would regard my conjecture as the ultimate in naive group selection, but the word "naive" might need to be dropped from this assessment (Sober & Wilson 1998; see also sect. 2.2 of Laland et al. with my reservations noted above)! My own assessment is that cultural systems may be far more explicable in terms of adaptive design than we currently appreciate. If so, then the adaptationist program can be a fertile source of hypotheses about human cultures, complementing Laland et al.'s approach, which is based more on the mechanics of the evolutionary process.

Authors' Response

Niche construction earns its keep

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Abstract: Our response contains a definition of niche construction, illustrations of how it changes the evolutionary process, and clarifications of our conceptual model. We argue that the introduction of niche construction into evolutionary thinking earns its keep; we illustrate this argument in our discussion of rates of genetic and cultural evolution, memes and phenogenotypes, cre-

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ativity, the EEA (environment of evolutionary adaptedness), and group selection.

R1. Niche construction

R1.1. Definitions. All living organisms take in materials for growth and maintenance and excrete waste products. It follows that, merely by existing, organisms must change their local environments to some degree. Niche construction is not the exclusive prerogative of large populations, keystone species, or clever animals, it is a fact of life. **Godfrey-Smith** is surely correct in his assertion that if evolutionary biologists neglect niche construction, it is not because they dispute that it does occur. The pertinent question, as Godfrey-Smith observes, is How does incorporating niche construction enhance our understanding of the evolutionary process?

We begin, at **van der Steen**'s request, with a clear definition of niche construction. A niche refers to the "occupation" of an organism; for example, to the ways in which an organism obtains its resources or defends itself in its environment, in contrast to its location or "address" in its environment, or habitat (Ehrlich & Roughgarden 1987). Our view is consistent with Hutchinson's (1957) concept of the niche as a multi-dimensional hypervolume. In theory, organisms can be decomposed into arrays of features (traits or characters), and environments can be decomposed into arrays of factors (Bock 1980). A feature of an organism is only an adaptation if and when it is matched to a specific selection pressure arising from an environmental factor at a particular location so that it increases the fitness of the organism at that address and moment; for example, if it permits more efficient acquisition of a food resource (Bock 1980).

Niche construction occurs when an organism modifies the functional relationship between itself and its environment by actively changing one or more of the factors in its environment, either by physically perturbing these factors at its current address, or by relocating to a different address, thereby exposing itself to different factors.

We further define two distinct sub-categories of niche construction. Organisms express *counteractive* niche construction when, by their actions, they either wholly or partly reverse a change in an environmental factor, and thereby restore an adaptive match between one or more of their own features and the altered environmental factor. Conversely, organisms express *inceptive* niche construction when they generate a change in an otherwise unchanging environmental factor by their own activities, or when they generate an additional change in an environmental factor that is already independently changing, thereby driving a feature-factor relationship into a new state. Our use of these terms does not, as **Bullock & Noble** and **Adenzato** suggest, carry a teleological connotation. Counteractive niche construction implies only that a novel selection pressure is counteracted by the actions of an organism. It is not intended to suggest that the processes that lead to the niche construction are necessarily teleological ones, although sometimes they may be (see sect. R2.2).

According to these definitions, **Godfrey-Smith** is right to query our talk of organisms "defining" their environment as niche construction, although there is a real sense in which organisms determine which factors are of relevance to them (Lewontin 1983). However, we dispute his criticism of our use of the word "choose." For example, choices of habitat are consistent with our definition, because relocations do change the factors to which an organism is exposed. It should now be clear to **van der Steen** that selection on moths, as he describes it, is not niche construction, but if swallows change either the environments of other swallows or their own social environments, then their activities do constitute niche construction. **Broude**'s description of niche construction as tailoring behavior to environments could not be further from our conception. Also unhelpful is Broude's description of "the niche construction hypothesis" as evolved responses to culturally based niche construction. This is just one possible consequence of niche construction, and it is not well described as *the* niche construction hypothesis.

Godfrey-Smith argues that the niche construction of past rather than present generations influences the selective environment. In fact, both may be relevant. Spider's webs, insect pupal cocoons, and caddis fly larvae houses modify the selective environments of the constructors. In contrast, bird's nests, female insect's oviposition site choices, and the soil transformed by earthworms also modify the environment of the constructor's descendants. The latter cases are all examples of ecological inheritance. We define as *ecological inheritance* any case in which an organism experiences a modified functional relationship between itself and its environment as a consequence of the niche-constructing activities of either its genetic or ecological ancestors (Odling-Smee 1988). Ecological inheritance is built into our theoretical models (Laland et al. 1996a; 1999), and, as described below, the addition of this second kind of inheritance system can make a considerable difference to the evolutionary process.

Adenzato argues that niche construction is not an alternative to standard evolutionary theory, because it is the product of natural selection. This is a distortion. Most other commentators, in particular **Aunger, Bowles, Robson Brown, Simonton,** and **Thompson,** clearly do see that niche construction is an extension (we do not claim it is an alternative) to standard evolutionary theory. From the beginning of life all organisms have, in part, modified their selective environments and their ability to do so is, in part, a consequence of their naturally selected genes. Adenzato's statement makes no more sense than the counter proposal that natural selection is just a product of niche construction! Niche construction and natural selection are two processes, operating in parallel, but also interacting.

R1.2. Niche construction changes the evolutionary process. Commentators **Russell & Carey** ask how niche construction changes the evolutionary process. **Bullock & Noble** express similar reservations about our view that niche construction is an important and neglected extension of the standard theory of selection, and **Wilson** questions whether this particular complexity is necessary. Let us summarise just three differences that this extension makes (more details are in Odling-Smee et al. 1996, and a formal mathematical analysis in Laland et al. 1996a).

The first difference is that traits whose fitness depends on alterable sources of selection (recipient traits) coevolve with traits that alter sources of selection (niche-construct-

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ing traits). This will result in evolutionary dynamics for both traits very different from what would occur if each trait had evolved in isolation. When ecological inheritance is involved, the evolution of the recipient trait depends on the frequency of the niche-constructing trait over several generations. Theoretical population genetic analyses have established that processes that carry over from past generations can change the evolutionary dynamic in a number of ways, generating timelags (e.g., in the 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 & Cavalli-Sforza 1976; Kirkpatrick & Lande 1989; Laland et al. 1996a; Robertson 1991).

The second difference is that acquired characteristics can play a role in the evolutionary process by their influence on the selective environment through niche construction. The Galápagos woodpecker finch provides an example (see Table 1 in target article). These birds create a woodpecker-like niche by learning to use a cactus spine or similar implement to peck for insects under bark. The finch's capacity to use spines is not inherited, but rather learned afresh by each individual. This learning certainly opens up resources in the bird's environment that would be unavailable otherwise and is therefore an example of niche construction. This behavior probably created a stable selection pressure favoring a bill able to manipulate tools rather than the sharp, pointed bill and long tongue characteristic of woodpeckers.

A third difference, that we have not stressed here since it relates to ecology, is that niche construction modulates and may partly control the flow of energy and matter through ecosystems. In ecosystem ecology this process is known as "ecosystem engineering" and it is currently receiving increasing recognition by ecologists (Jones et al. 1997).

These points help justify our argument that the introduction of niche construction into evolutionary accounts has the potential to advance theoretical and empirical work in biology. In the following sections we argue that a niche construction perspective is particularly valuable in the study of human evolution.

R2. Clarifying our "multiple-processes in evolution" perspective

In section 1.3 of our target article we suggested that, in humans, adaptive information may be acquired through at least three knowledge-gaining processes (genetic evolution, learning, and culture), and we emphasized that this information underpins niche construction. In this section we clarify a number of points related to this perspective.

R2.1. Niche construction is not genetically determined. In spite of our emphasis on learned and culturally transmitted niche construction, three of the commentators (**Aunger, Broude,** and **Gabora**) appeared to believe that we were suggesting that human behavior, niche construction or culture are exclusively based on genes, or that they are genetically determined. Broude even concluded that we wish to "resuscitate the kinds of adaptive explanation to which conventional evolutionary psychologists object," and presumably that early sociobiologists advocated. This was far from our goal. In fact, we agree with much of what these commentators have to say on this matter. For instance, Aunger argues that there are cultural selection and mutational forces that have a degree of independence from genetic control, while Gabora maintains that behavior cannot be explained exclusively in terms of genetically-driven selection. We agree with both these statements. In section 2.3 of our target article we state that culture "can lead to the transmission of information that results in a fitness cost relative to alternatives." This is effectively saying that cultural processes are not necessarily subject to the constraints of genes or biological fitness. The cultural transmission parameters in the cultural evolution and gene-culture coevolutionary mathematical models with which all three of us have worked, are formally equivalent to treating cultural transmission as based on cultural replicators that are distinct from genes (Cavalli-Sforza & Feldman 1981; Feldman & Cavalli-Sforza 1976; Feldman & Laland 1996). Culture is not "a patsy to natural selection" (Aunger), nor do we suggest that all behaviors and other components of culture are completely independent of genes or development.

R2.2. "Smart" versus "blind" variants. We think of genetic processes, ontogenetic processes, and cultural processes as operating at three distinct but interconnected levels. Each level is informed, but not completely determined by the others: that is, learning is constrained, but only loosely, by genetic information, and cultural transmission may be constrained, but not completely specified, by both genetic and developmental processes. In addition, ontogenetic processes, particularly asocial learning, may also be affected by culture, as **Gabora** implies when she says social and asocial learning are impossible to disentangle, and as **King** indicates in her comments on the co-construction of tool-using behavior in chimpanzees. We suspect that a misunderstanding of the relationship between these processes underlies **Broude**'s misinterpretation.

Unlike **Simonton,** and Campbell (1965) on whom Simonton bases his model, we also believe that the Darwinian process selects only "blind" or random variants at the genetic level. Learned behavior may be broadly Darwinian in character, as Plotkin and Odling-Smee (1981) and Dennett (1995) suggest, but it is not based on the selection of randomly-generated behavior patterns. This is because the perceptual systems, the motivational systems and the behavioral systems in individual organisms are all biased by, but not determined by, their genes. Thus "smart" rather than "blind" variants are selected by the learning process. Similarly, human beings do not create or adopt cultural variants (or memes) at random, because past phylogenetic and developmental processes, including past learning, inform these creative and selective processes. **Gauvain** agrees with us that developmental processes provide important links between biological and cultural evolution, yet feels we have underplayed the influence of these processes. In general, we agree that an understanding of developmental processes can shed light on the evolutionary process (Bateson 1988).

Criticisms by **Bullock & Noble** of our use of teleological language needs reconsidering here. In one respect we believe teleological language can sometimes be justified at every level except the genetic because, as **Bullock &**

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Noble themselves state and as **Gauvain** also emphasizes, learning and cultural processes are often goal directed processes. Thus niche construction that is based on either learned or culturally transmitted information may be expressed by an organism "intentionally" relative to a specific goal.

Townsend asks how we explain intra-cultural variation, for example, differences between the sexes or between different social classes. As Townsend appears to anticipate, it is partly to account for such data that we have stressed how genes and learning help to shape the cultural information that individuals acquire and express. Also, different kinds of information may be culturally transmitted from and to different sub-sections of societies. Moreover, genotypic, learned, and socially transmitted differences may interact to generate further intracultural variation. We agree with Townsend that culturally transmitted traits may be adaptive (i.e., may increase reproductive success) for some classes of individual and maladaptive for others.

Lipp advances his own theory that encephalisation leads to rapid evolution, following buffering of genetic variation from selection. We are not qualified to assess the neuroscientific basis of his particular argument. It is a widely held view that developmental plasticity can shield genetic variation from selection, although in other circumstances it can do the opposite (Schlichting & Pigliucci 1998). However, the relationship between developmental plasticity and rate of evolutionary change is not straightforward and empirical studies have found that the evolutionary divergence of traits is not necessarily related to their plasticity (Schlichting & Pigliucci 1998; Stearns 1983). The lack of a clear relationship may reflect the fact that plasticity both reduces the efficacy of natural selection and increases the capacity for niche construction, which in turn allows organisms to create new niches, exposing themselves to novel selection pressures. Although our perspective leaves us sympathetic to Lipp's argument, the issue of how plasticity affects selection is a problem to which evolutionary biology has yet to provide a comprehensive answer.

R2.3. Social learning and cultural evolution. Asocial learning is a part of culture, argues **Gabora.** We agree that learning is central to an understanding of culture, but prefer to think of asocial learning as a separate process. For us, the role of asocial learning in cultural evolution is in many respects analogous to the role of mutation in biological evolution (Cavalli-Sforza & Feldman 1981); that is, it is one of the processes that create variants on which selection may operate. Mutation is an important process in evolution, but it is not the same thing as natural selection. Similarly, asocial learning is critical to cultural change, but it is not the same thing as social transmission (or cultural selection).

Aunger states that some of the "mental machinery" underlying cognition is culturally constructed. We agree. It is clearly the case that individuals in part learn how to think, what to think about, and which ideas to accept through their culture. However, this is not the whole story, and individual differences in susceptibility to particular memes may reflect differences in genotype and development.

Gauvain and **King** both stress how each group member helps create the shared knowledge of a group, and frequently shape it in ways that meets each individual's own interests. This is an interesting point, which we would characterize as a form of social niche construction. For humans, as well as many other species, an important part of the environment is the social environment, which is just as subject to niche construction as is the ecological environment.

According to **Saidel,** we believe cultural evolution is a sub-species of niche construction. We do not. For humans, cultural information may be expressed in niche construction, but that does not make cultural evolution the same thing as niche construction. Cultural evolution is a term that loosely describes the process of cultural change. It implies nothing about biological evolution or niche construction, although we believe that cultural and biological evolution may interact in complex ways, and that both genes and cultural traits may influence how humans do niche construct. Cultural inheritance is also distinct from ecological inheritance. The former refers to the transmission of learned information from one generation to the next, the latter to the "inheritance" of a modified ecological environment. In spite of this disagreement we believe Saidel's overall position is very similar to our own.

R3. Human adaptation and evolution

In this section we use the multiple-processes framework described in our target article, and clarified in the previous section, to address a number of issues raised in the commentaries pertaining to human adaptation and evolution.

R3.1. Rates of genetic and cultural evolution. Genetic evolution is too slow, **Adenzato** implies, and cultural change too fast for the latter to drive the former. **Colarelli** says culture is not stable enough to cause genetic evolution and that niche construction adds further instability. In fact, selection experiments and observations of natural selection in the wild have led to the conclusion that biological evolution may be extremely fast, with significant genetic and phenotypic change sometimes observed in just a handful of generations (e.g., Dwyer et al. 1990; Grant & Grant 1995; Reznick et al. 1997; Thompson 1998). **Lipp** describes a selection experiment in mice that reveals a major brain restructuring in just three to four generations. His finding is consistent with many other selection experiments carried out over the last century. Rates of genetic change vary enormously according to the nature of the genetic effects on the selected phenotype (Hartl & Clarke 1989), but most evolutionary biologists would agree that biological evolution does not always require millions of years. The distinction between ecological and evolutionary time scales has been blurred (Thompson 1998).

Observations of hominid stone tool technologies reveal that cultural change can be extremely slow. As **Bowles** points out, cultural institutions such as labor markets can also be extremely persistent, albeit on a shorter timescale. Furthermore, theoretical analyses have revealed that cultural transmission may change selection pressures to generate unusually fast genetic responses to selection in humans (Feldman & Laland 1996). Thus it is feasible that genetic and cultural evolution could operate at similar rates. In fact, the past two million years of human evolution is arguably best regarded as a period of gene-culture coevolution (Feldman & Laland 1996).

Relative to the same two million year period, we were pleased to see **Robson Brown** taking up our suggestion that it might be possible to identify "genetic signatures" relating to cultural events, and then use identified signatures

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to trace the history of specific cultural activities, such as the use of fire or the spread of agriculture, across human groups. We had realised that this approach is already in use, but we are pleased that Robson Brown agrees that our niche construction model could take it a step further. As Robson Brown clearly appreciates, we predict relationships between cultural traits and genetic signatures only where there is appropriate niche construction. Neglect of the contingency of this relationship may partly explain the poor correspondence between genetic and cultural phylogenies. Looking for genetic signatures will not be easy. For instance, in the Kwa example (sect. 2.1.1, last para., of our target article), it would have been difficult for anyone to predict a priori that when the Kwa cut down trees to create clearings for their yams, they were eventually going to affect the frequency of the sickle-cell allele in their population. However, useful genetic signatures may be discovered in other species (e.g., fire-prone or agricultural plants). With the growing power of molecular techniques, using genetic signatures to track such cultural events could become an important tool in the study of hominid evolution.

Cultural niche construction can, of course, cause rates of environmental change that really are too fast for human genetic evolution to track, and it is probably doing so increasingly. In fact, in the last 25 to 40 thousand years the dominant mode of human evolution has probably been cultural. However, that does not mean there has been no evolutionary feedback from niche construction: it merely switches the evolutionary responses to the cultural domain. Under such circumstances, cultural niche construction should have favoured further cultural transmission or coevolution between culturally transmitted characters.

R3.2. Memes and phenogenotypes. Both **Aunger** and **Gabora** suggest that we do not place enough emphasis on memes. They suggest that memes are distinct replicating units, that memes can evaluate and produce other memes, that memes introduce new selectional processes and generate new kinds of variation, and that genetic and cultural phenotypes do not necessarily pass through the brain in tandem. We agree with most of this, although we prefer not to use language that implies that memes are independent living entities. Our own focus on phenogenotypes was with regard to human evolution. When it comes to understanding human culture, most of the dynamics are best understood in terms of cultural evolution, with the proviso that developmental processes filter meme creation and selection. We remind these commentators that all of us have developed cultural evolution models, and one of us (Feldman) is a coauthor of a well-known book on this topic (Cavalli-Sforza & Feldman 1981). If cultural evolutionary models do not use the term "meme," it is because they were first developed a few years before the term meme was coined (Cavalli-Sforza & Feldman 1973). To the extent that "cultural traits" equate to "memes," we are strong advocates of a future science of memetics, and believe cultural evolution and gene-culture coevolutionary models could provide a solid theoretical foundation for that science.

Aunger is mistaken when he suggests that "real" dual-inheritance (genes and culture) occurs without phenogenotypes. If genetic and cultural inheritance are fully independent then we can study each process alone using population genetic or cultural evolutionary models. That is not dual-inheritance but two kinds of single inheritance. If the two inheritances interact, we should only study them using phenogenotypes, since there is no alternative that will not introduce distortions. Aunger's mistake stems from a misunderstanding of the phenogenotype concept. The use of phenogenotypes does not imply that the adoption of cultural traits is constrained by genes. Phenogenotypes refer to classes of individuals, with a combination of genotype and cultural trait. They represent the basic evolutionary unit when both biological and cultural selection processes are operating in association. Focusing on phenogenotypes is critical to dual-inheritance systems, because they allow all selection (be it natural or cultural selection) to occur between phenogenotypes. Treating cultural and biological processes as independent would ignore any non-random associations between genotypes and cultural traits. Phenogenotypes are merely the *currency* for dual-inheritance models. That is, if genes and culture are evolving together, we have to track phenogenotypes if we are to understand this coevolution. This is true even when cultural traits are subject to evolutionary forces acting independently of genes (Aunger). **Pocklington** makes the same mistake with his suggestion that the phenogenotype concept is a form of naive group selection. Tracking phenogenotypes is no different from tracking gametes in two-locus population genetics models: they are the simplest entities that take account of interactions between the two loci. Is all two-locus population genetics group selection?

Pocklington's suggestion that non-vertically transmitted cultural characters are necessarily decoupled from genes, is also misguided. Gene-culture coevolution may occur under any mode of cultural transmission. Provided the cultural traits are transmitted from one generation to the next, it does not matter whether offspring learn from parents, teachers, older siblings, or peers although rates of evolution depend on the mode of transmission. Moreover, provided the cultural environment imposes selection on genotypes, the phenogenotype remains the only appropriate currency for analysis.

Pocklington criticizes our emphasis on vertical cultural transmission, and argues that there is little transmission of acquired information from parents to offspring. There may be more cultural knowledge transmitted from parents to offspring than Pocklington believes, but we would welcome detailed empirical analyses. Pocklington acknowledges that family, kinship, and social stratification traits probably have strong vertical transmission components, and other vertically transmitted traits have been documented (Boyd & Richerson 1985; Cavalli-Sforza et al. 1982). However, the mode of transmission is not at all central to our hypotheses. Most of our arguments concerning vertical transmission require only transgenerational transmission, and relate to the temporal distance between the learning of transmitter and receiver. For instance, there is usually a generation between parents and offspring learning a particular skill, while peers or siblings learn skills at more similar times. It is this temporal factor that is important to our hypotheses. If the environment, including the social environment, is stable from one generation to the next, it will pay one generation to learn the same things as the previous generation, irrespective of whether the transmission is from parents, teachers, or peers. **Townsend** clearly sees the value of this particular temporal perspective on cultural transmission.

Gauvain and **King** both stress that social learning is a

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constructive and interactive process. This is undoubtedly true, and may constitute a part of the niche construction story. Their argument that social learning usually occurs at a particular stage in development is well taken. A cultural evolution model with time-dependent social learning might address some of their concerns.

Gabora's suggestion that no two versions of a meme are the same is potentially problematic for cultural evolution models, but much depends on the fineness of the scale being used to define the memes. Perhaps meme and cultural evolution enthusiasts alike should focus on those cultural units that appear to be relatively consistently expressed in different individuals, and that appear to have a "core essence" that is stably transmitted and/or reconstructed.

R3.3. Creativity and innovation. An interesting hypothesis is proposed by **Simonton** concerning how niche construction might drive the evolution of creativity, which meshes extremely well with the ideas concerning the evolution of culture spelled out in section 2.1.3 of our target article. Evidence from studies of innovation in primates supports Simonton's hypothesis. It is plausible that the ability to learn from others and to generate novel behavior patterns have co-evolved throughout primate evolution. Consistent with this is evidence that the incidence of innovation and social learning co-vary across primates, each correlating with relative brain size (Reader, personal communication). Primate innovation often occurs in response to environmental challenges such as drought or habitat destruction (Kummer & Goodall 1985; Lee 1991). If more innovative individuals are at an advantage in responding to the challenges imposed by the self-modified niches, selection may favor enhanced creativity.

Another feature of **Simonton**'s argument, which is consistent with studies of innovation in animals, is that human creativity is positively associated with independence and nonconformity. Evidence is beginning to emerge that animal innovators are sometimes individuals for which the current prevailing risk-averse foraging strategies are unproductive, and which are driven to search for alternatives (Reader, personal communication). Primate studies appear to indicate that innovators are frequently low in rank or poor competitors that occupy the periphery of the social group (Kummer & Goodall 1985). These observations support the notion that there are stable personality and class differences in the propensity of individuals to create novel behavior patterns, and that the innovators are not typically the dominant members of society.

Sternberg correctly notes that if conformist cultural transmission is operating, some process must counteract it to generate novel behavioral variants, otherwise cultural evolution would cease. The same is true of the conventions described by **Bowles.** We accept as plausible Sternberg's notion that much innovation comes from creative, nonconformist individuals. However, as detailed above, a large part of innovation is of the "necessity is the mother of invention" type. It would therefore seem that creativity is probably confounded with "desperation." Similarly, intelligence, as defined by Sternberg ("goal-directed adaptive behavior") in part depends on the ability to act, which is constrained by others when there are limited resources. Here intelligence is probably confounded with power and dominance. Studies of the diffusion of innovations in human populations suggest that there is a critical stage for any novel trait when the "early adopters" (opinion leaders, role models, dominant elite) take up the new behavior invented by "innovators" (risk prone, low status), and the majority of the rest of the population follows in their wake (Rogers 1995). Such an innovation is therefore selected for by conformist transmission. **Gabora** raises a separate issue by stressing that creativity can come from meme recombination among groups of people, as well as from the innovation and learning of a single individual. This too is a valid point.

R3.4. Problems with the EEA. Several commentators (**Adenzato, Barkow, Colarelli, Townsend**) stress the Environment of Evolutionary Adaptedness, the EEA, and of those psychological mechanisms that evolved in it, as central to understanding human behavior and culture. They argue that the human mind was fashioned for a past world of hunting and gathering on the African plains in the Pleistocene (Tooby & Cosmides 1990). They reason that since modern human environments are so different from the EEA, humans should no longer be expected to behave in an adaptive manner, but that we can nevertheless understand much modern human behavior by evoking the EEA, and using that as a source of interpretation. We see a number of difficulties in this approach.

The main problem with the EEA is that it is not a very useful concept. As comparatively little is known about the lifestyle of our ancestors throughout the EEA, it has engendered a wealth of undisciplined speculation and story telling in which virtually any attribute can be regarded as an adaptation to a bygone stone-age world. The EEA concept also implies that the Pleistocene hunter-gatherers exhibit little variability in time or space, which is manifestly false when one considers that stone-age peoples lived not only on the African savannah, but in deserts, next to rivers, by oceans, and in forests (Boyd & Silk 1997; Foley 1996). Even for Homo sapiens, the first E in EEA is likely to have been enormously variable.

Daly and Wilson (1999) rightly point out that much of the dissatisfaction with the EEA has derived from its equation with stereotypical Pleistocene savanna. They recommend that enthusiasts utilise the definition of Tooby & Cosmides (1990, pp. 386–87): The EEA concept does not refer to a single "place or habitat, or even a time period. Rather, it is a statistical composite of the adaptation relevant properties of the ancestral environments encountered by members of ancestral populations, weighted by their frequency and their fitness consequences." The trouble is, this is not an operational definition. Human ancestors can be traced back to the origins of life. Some human behavioral adaptations such as maternal care, or a capacity to learn, may even have evolved in our invertebrate ancestors. Many perceptual preferences will also be phylogenetically ancient. Much social behavior, such as forming stable social bonds, developing dominance hierarchies, and co-ordinated hunting evolved in our pre-hominid primate ancestors. Deliberate deception, a theory of mind, and a capacity for true imitation probably evolved in pre-hominid apes. Yet if researchers are going to use the EEA, they need to identify a particular time period and class of ancestor. In principle, EEA supporters could carry out a phylogenetic analysis to determine the earliest known ancestor exhibiting a particular trait. In practice, this is never done, and because little is likely to be known about that particular ancestor, it would be an extremely time-consuming exercise resulting in very

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vague speculations about the origins of a human faculty. No wonder then, that evolutionary psychologists resort to a stereotype.

A second problem for the EEA argument is that, at best, it can be only partly true. Human beings cannot be exclusively adapted to a past world, and not at all adapted to modern life, otherwise we would be extinct. Our capacity continuously to create solutions to the self-imposed problems caused by our niche construction reflects the fact that humans are very adaptable creatures. The flexible nature of our learning and culture allows us to survive and flourish in a broad range of environmental settings. That adaptability means that rather than being adapted to a particular environment, humans adapted to a broad range of potential environments. In section 2.3.2 of our target article, we made the argument that because organisms construct significant components of their environments, as they evolve they may effectively drag part of their environments along with them. **Barkow** puts a clever twist on the EEA argument, saying that to the extent that cultures are similar, cultural niche construction may be similar, leading to selection for panhuman evolved psychological mechanisms, and acting as a barrier to the evolution of genetic differences between peoples. There may be something to this argument. Human niche construction is strikingly divergent, but there may be some "hidden commonalities" among overtly different culturally constructed niches. We would also agree with Barkow that if modern cultures have "hidden commonalities" with those of our ancestors, then we may be better adapted to our contemporary societies than some might imagine.

Colarelli raises a "criterion problem" that also relates to the EEA. If evolution occurs not just at the genetic level, but perhaps at the ontogenetic and cultural levels as well, how do we know what is an adaptation? This is a good question. However, Colarelli's solution is to pretend the complexity is not there. He begins by claiming that evolutionary theory does not have a criterion problem, since adaptations are judged with the currency of fitness. But measurement of fitness is not straightforward. In a recent authoritative text, Endler (1986, p. 33) writes, "there are many different definitions and measures of fitness" and reduces the multitude of terms and methods to a core five concepts. Colarelli argues that assessing the value of a trait is reasonably straightforward, yet there are genuine problems in determining which characters are traits, and which traits are adaptations (Gould & Lewontin 1979; Lewontin 1979). We see no virtue in pretending that evolution is a simpler process than it actually is. Simple-minded evolutionary storytelling alienates many more human scientists than it draws into the evolutionary fold. Undoubtedly humans exhibit "evolved psychological mechanisms." However, the EEA concept does not promote good science, and there are better ways to incorporate evolution into the human sciences.

R3.5. Group selection. Both **Wilson** and **Thompson** criticise our section on co-operation for implying that kin selection, reciprocal altruism, and group selection are different processes. This was not our intention. We accept that both kin selection and reciprocal altruism can be redescribed as group selection, in fact one of us (Feldman) made precisely that point 20 years ago (Uyenoyama & Feldman 1980; Uyenoyama et al. 1981). We also accept that the theoretical plausibility of group selection is well established (Price 1970), although Wilson is surely correct in his claim that professional biologists have been slow to appreciate this (Sober & Wilson 1998). However, the conditions under which the group selection of genes will be influential are considerably more stringent than Thompson suggests in his article, requiring not just a positive relationship between the group productivity and the frequency of altruists within groups, but also that this covariance has a greater effect on the change in frequency of the genes underlying altruism than within-group selection, and that an appropriate demographic structure maintains genetic differences between groups. Besides kin selection and reciprocity, we remain sceptical as to how much group selection of genetic variation actually occurs in nature, but this is an empirical issue.

Wilson also complains about our distinguishing Boyd and Richerson's (1985) group selection of cultural variants from his Multiple-Level-Selection (MLS) framework. We had not appreciated that Wilson had embraced Boyd and Richerson's model into his (and Sober's) scheme when we wrote our original article. To the extent that Sober and Wilson are saying that same thing as Boyd and Richerson, we are in agreement. However, it does not follow that because we support Boyd and Richerson's model we necessarily accept the whole MLS story. For the reasons outlined in our target article, when it comes to accounting for large-scale human co-operation, we believe there are good theoretical reasons for anticipating that the group selection of cultural variants is a more compelling explanation than the group selection of genetic variants. Our scepticism concerning the latter stems not just from the eroding effects of selection within groups, or the size of human groups, as **Thompson** suggests, but also from the gene-flow between groups that weakens group differences. For example, where there is conflict between hunter-gatherer groups, some of the defeated peoples are likely to be absorbed into the conqueror's group (Soltis et al. 1995). Theoretical treatments have raised the possibility that punishment or coercion may maintain group differences, but it is not clear that they favour co-operation (Boyd & Richerson 1992). **Bowles** stresses how conventions can generate and maintain cultural differences between groups, and that cultural processes other than conformist transmission can act in this manner. Nevertheless, to the extent that social processes such as gossip, pressure to conform, and conventions operate to maintain group identities and prevent cheating, we regard them primarily as barriers to cultural rather than genetic variation. Nevertheless, it is possible that genetic variants may be selected as an indirect consequence of the group selection of cultural traits.

Wilson criticises our O_1/O_2 heuristic applied to co-operation and conflict as underspecified. This is true, albeit slightly unfair, as verbal heuristics are always underspecified, and our goal in this paper was to avoid formal models. Our point was simply that taking a niche construction perspective may give insights into the conditions under which co-operation might be favoured. In spite of Wilson's assertion to the contrary, we feel that it is implicit in our writing (e.g., Laland et al. 1996a) that we were referring to relative rather than absolute fitnesses; that was certainly our intention. (Ironically, group selection is one form of selection for which tracking relative fitness is not enough, and absolute fitnesses at some level must also be taken into account.) Perhaps a clearer specification would be the following:

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> Any organism, O_1, should be prepared to co-operate in ways that benefit any other organism, O_2, provided that the total niche-constructing outputs of O_2, or any of O_2's descendants, modify resources in the environment of O_1, or any of O_1's descendants, in such a way that fitness benefits to O_1 exceed the cost of O_1's co-operation, and increase O_1's fitness relative to other members of O_1's population that do not niche construct in the same manner.

We applied our O_1/O_2 heuristic primarily to interactions between individuals. However, we did raise the possibility that the scheme may also apply to some situations in which O_1 and O_2 are groups, although we were careful to stress that this is likely to be restricted. In spite of our reservations, we accept enough of what **Wilson** and other group selection supporters are saying to recognise that niche construction could possibly make group selection more likely. **Thompson** has clearly picked up on this, and makes a number of interesting suggestions.

R4. Closing statement

In writing the target article, our goal has been to provide a more useful and more acceptable evolutionary framework for the social and other human oriented sciences (henceforth the human sciences) than standard evolutionary accounts. We believe that, hitherto, there have been two principal reasons why many human scientists have found it difficult to make use of evolutionary theory. One is that the theory appears to have too little to offer them. Human scientists are predominantly interested in phenotypes, namely human beings. Chiefly they are concerned with what humans do, with economic and social activities, with the inheritance of property, and with other aspects of cultural inheritance. They are far less interested in genes and genetic inheritance, except with respect to individual human development rather than human evolution. Although the origins of evolutionary theory reside in the study of phenotypes and their variation, much of modern theory and practice has focussed on genes and their inheritance rather than phenotypes. In fact, in recent years, conventional evolutionary theory has if anything, been further downplaying the role of phenotypes, sometimes reducing phenotypes to mere "vehicles" for their genes. These biological priorities are probably unattractive to the majority of human scientists because they do not appear to offer the human sciences any useful point of contact with evolutionary theory.

One reason why we believe our framework may appeal to human scientists is that, in adding niche construction to evolutionary theory, we are proposing an additional role for phenotypes in evolution. Humans are not just passive vehicles for genes, they also actively modify sources of natural selection in environments. It is abundantly obvious that humans do niche construct, and any evolutionary theory that formally acknowledges this fact is likely to be more in tune with most human scientists' thinking. Also, because the niche construction of complex organisms such as humans depends so heavily on developmental processes, learning, and culture, which are the subject matter of the human sciences, it follows that human scientists may not only derive benefits from placing their own subjects in an evolutionary context, but they may also make real contributions to our understanding of human evolution. **Bowles** anticipates this point by seeing potential connections between human cultural niche construction, human labor markets, and human economic institutions. We are particularly grateful for his contribution because we have not yet developed our theory far enough to encompass the kinds of human institutions that are the principal concern of many human scientists. **Bowles** is probably right; it should be possible to develop evolutionary theory further in this direction.

The other reason why human scientists have difficulty with evolution is the simplicity versus complexity issue that was raised by several commentators (**Bullock & Noble, Colarelli, Russell & Carey, van der Steen, Wilson**). As both Wilson and Colarelli point out, adaptationist approaches to conventional evolutionary theory enjoy the advantage of being relatively simple, and their simplicity is regarded as a virtue because it allows shortcuts to the development of hypotheses and the drawing of conclusions. However, for many human scientists, the theory is too simple, and for that reason, as Russell & Carey note, it repels many of them. Adding niche construction inevitably makes evolutionary theory more complicated and any extra complexity must earn its keep, otherwise adding it would be pointless. However, in the human sciences we believe the extra complexity introduced by niche construction is necessary, and that it will be seen to earn its keep as soon as human scientists start using it in new ways.

Two of the commentaries can be used to illustrate this point. We disagree with **Bullock & Noble**'s proposition that science is exclusively concerned with reducing the number of hypotheses. **Robson Brown** draws attention to the fact that by increasing the number of evolutionary explanations for the initial speciation event that resulted in the hominid family, we may be contributing something new to the debate over definitions of species, particularly hominid species. This is both a reply to Bullock & Noble, and exactly the kind of discussion we want to encourage.

Russell & Carey stress that human scientists will need convincing that there is something for them in our model at the "workface" level at which they go about their business. That is exactly right. We are therefore delighted that so many of the commentators were willing and able to use ideas in our framework as a stimulant to their own research programs. Russell & Carey also ask for specific predictions and hypotheses for the human sciences. Such predictions can be found throughout our target article. However, the fertile nature of the niche construction perspective is beautifully illustrated by the commentaries of **Barkow, Bowles, Robson Brown, Simonton,** and **Thompson,** all of whom have started to use niche construction in fresh ways to develop their own particular hypotheses.

The evolutionary framework in this article is not itself designed to be a single theory that can be subject to empirical test, or modeled formally. Rather it is a broad conceptual model, designed to act as a hypothesis-generating framework around which human scientists can structure evolutionary approaches to their disciplines. The complexity of the processes involved in human evolution is not problematic if it is possible to extract from this conceptual model particular subprocesses, or derive specific hypotheses, that are subject to empirical test, and can be developed into formal models. Researchers may choose the levels or processes in the model that they feel are most appropriate, but they will have the advantage of working within the context of a rich overarching framework. Our framework does not dictate a particular research methodology (when it comes to theoretical ap-

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proaches we see advantages to using dynamic models) but the simulation methods advocated by **Bullock & Noble,** and many other approaches, are also likely to be instructive.

Finally, we are grateful to all our commentators for taking the time to write their articles and for their stimulating comments. We thank them and hope that others will see that there are rich opportunities for using evolutionary theory in the human sciences in a manner that goes well beyond storytelling. In the long term, we would like to see a greater integration of evolutionary theory and the behavioural sciences, and hope that our conceptual model will be regarded as contributing to that integration.

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Letters "a" and "r" appearing before authors' initials refer to article and response, respectively.

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