EVOLUTION

PERSPECTIVE:
SEVEN REASONS (NOT) TO NEGLECT NICHE CONSTRUCTION

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Abstract.—The niche-construction perspective within evolutionary biology places emphasis on the changes that organisms bring about in their selective environments. Advocates of this viewpoint argue that there is both accuracy and utility in treating niche construction as an evolutionary process in its own right, rather than merely as a product of evolution. Here we discuss and assess seven putative weaknesses of the niche-construction perspective. Niche construction has been neglected or rejected on the grounds that (1) it is not prevalent, (2) its study is not tractable, (3) it is not a process, (4) it is caused by natural selection, (5) it does not change our understanding of evolution in any fundamental way, (6) it does not bring about adaptation, and (7) it is not a single phenomenon. In each case, we critically evaluate the theoretical standing of these arguments and consider the empirical evidence that can be brought to bear on the debate. We conclude that none of these are strong criticisms of the niche-construction perspective and maintain that there are compelling reasons for treating niche construction as a major evolutionary process.

Key words.—Adaptation, ecological inheritance, evolution, extended phenotype, inheritance, niche construction.

The Niche Construction Perspective

The niche-construction perspective was introduced to evolutionary biology in the 1980s through a series of seminal essays by Richard Lewontin (1982, 1983, 2000), and has gathered momentum over recent years (Brandon and Antonovics 1996; Laland et al. 1996, 1999, 2001; Odling-Smee et al. 1996, 2003; Odling-Smee 1988; Oyama et al. 2001; Lewens 2003; Sterelny 2003; Boni and Feldman 2005; Donohue 2005). Niche construction is the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or others' niches (Odling-Smee et al. 2003). For instance, numerous animals manufacture nests, burrows, holes, webs, and pupal cases; plants change levels of atmospheric gases and modify nutrient cycles; fungi and bacteria decompose organic matter; bacteria fix nutrients (for a review of this literature, see Odling-Smee et al. 2003). However, the defining characteristic of niche construction is not organism-driven modification of the environment per se, but rather modification of the relationship between an organism and its relative niche (Odling-Smee 1988). Hence the term ''niche construction'' includes such cases as habitat selection, where organisms relocate in space to modify the environments that they experience (Cody 1985; Rosenzweig 1991; Hanski and Singer 2001).

Advocates of the niche-construction perspective are concerned with the causal basis of the organism-environment match and its inherent symmetries, and the active role that organisms play in driving evolutionary and coevolutionary events. They seek to explain the adaptive complementarity of organism and environment in terms of a dynamic, reciprocal interaction between the processes of natural selection and niche construction. Evolution is based on networks of causation and feedback in which organisms drive environmental change and organism-modified environments subsequently select organisms.

Niche-construction theory contrasts with conventional conceptualizations of evolution. In standard models, leaving aside complications such as coevolution and habitat selection, adaptation is a process by which natural selection shapes organisms to fit preexisting environmental ''templates.'' The causal arrow points in one direction only: environments, the source of selection, determine the features of living creatures. According to George Williams (1992, p. 484): ''Adaptation is always asymmetrical; organisms adapt to their environment, never vice versa.''

The distinction between this evolutionary perspective and that emphasizing niche construction is illustrated by the familiar example of the beaver. Standard evolutionary theory

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models the evolutionary consequences of beaver dam building in the same way as other aspects of beaver phenotypes: solely in terms of fitness ''payoffs'' to the underlying genes; that is, it recognizes that selection has favored dam-building alleles over their (now defunct) alternatives. Dam building is an extended phenotypic trait (Dawkins 1982), but a central theme of Dawkins's argument is that extended phenotypic adaptations are no different from any other adaptations. The extended phenotypic perspective has the advantage that dam building, and niche construction in general, can be treated in the same manner as adaptations expressed inside the body of the gene carrier.

Advocates of the niche-construction perspective regard this stance as unsatisfactory, both because it misses part of the causal story and because it discourages consideration of certain forms of selective feedback within evolution. When a beaver builds a dam and lodge, creating a lake and influencing river flow, it not only affects the propagation of dam-building genes but it dramatically changes its local environment, affecting nutrient cycling, decomposition dynamics, the structure of the riparian zone, and plant and community composition and diversity (Naiman et al. 1988). It follows that beaver dam building must also transform selection acting on a host of other beaver traits, influencing subsequent beaver evolution. The active agency of beavers in constructing these modified selection pressures and thereby acting as codirectors of their own evolution (not to mention that of other species) currently goes unrecognized.

The beaver is hardly unique. Termites live in massive structures that equilibrate temperature and humidity, resist physical disturbance, and exclude all but the most specialized of predators (Hansell 1984; Pearce 1997). Termites inhabit mini-universes that they have partially constructed themselves. There is a fit between termites and their world, but not solely because termites have unidirectionally adjusted to their world, but because they have in part adjusted their world to fit them. As Turner (2000) has shown, almost every aspect of termite biology depends on their mound building, for these structures profoundly modify subsequent selection pressures.

Often the modifications produced by niche-constructing organisms persist for longer than the individual constructors, continuing to modulate the impact of environment on subsequent generations of the population, a legacy described as an ''ecological inheritance'' (Odling-Smee 1988). Modified selection pressures will remain in the beaver's environment just so long as the dam, lake, and lodge remain. Given that dams are frequently maintained by families of beavers for decades (Naiman et al. 1988), that could be considerably longer than the lifetime of an individual beaver. Likewise a single mound system can last many termite lives. Moreover, the habits of dam and lodge building, once begun, and once they survive an initial selective sieve, result in a permanent alteration of the *kind* of environment that beavers, and hence other beaver genes, experience. Once those genes expressed in dam building have become common, there is a change in the typical environment in which other beaver genes exert their phenotypic effects, a change routed via the effects of dam making on beaver selective environments. From the niche-construction perspective, offspring inherit two legacies

from their ancestors, genes and a modified selective environment.

It is frequently possible to study this feedback from the conventional standpoint, using tools such as models of habitat selection, maternal inheritance, indirect genetic effects, or phenotypic plasticity (Rosenzweig 1991; Via et al. 1995; Mousseau and Fox 1998a,b; Schlichting and Pigliucci 1998; Wolf et al. 2000; Rice 2004). We regard these theoretical developments as extremely encouraging. Such work illustrates the conceptual and mathematical tools that can be applied to study the rich evolutionary interactions between organisms and environments. Nonetheless, the magnitude and significance of niche construction remains underappreciated, in part because standard evolutionary theory does not encourage attention to such phenomena (Odling-Smee et al. 2003; West-Eberhard 2003).

Most evolutionary biologists devote little consideration to the causal role of the organism in evolution or multigenerational feedback from extended phenotypes. To the extent that such factors are recognized at all, they are commonly perceived as insufficiently important to challenge a conventional perspective that is widely regarded as functioning effectively, and which has the undoubted merits of familiarity and simplicity. Instead, evolutionary biologists and ecologists have devised a set of theoretical tools for dealing with the feedback generated by niche construction on a piecemeal basis within the framework of standard evolutionary theory.

As this debate gathers momentum, it is timely to consider in detail the commonly expressed reasons against adopting the niche-construction perspective. Here we present, and critically evaluate, seven such alleged weaknesses of the niche-construction viewpoint. Although some of these reservations about niche construction are in the literature, others have mostly been made verbally. Niche construction has been neglected on the putative grounds that (1) it is not prevalent, (2) its study is not tractable, (3) it is not a process, (4) it is a mere effect of natural selection, (5) it does not change our understanding of evolution in any fundamental way, (6) it does not bring about adaptation, and (7) it is not a single phenomenon. Based on published articles, reviewers' comments and verbal discussion, we judge these seven issues to lie at the heart of the controversy. In framing our discussion of the topic in this criticism-response manner, we do not imply that the proponents of niche construction have been unfairly treated. To the contrary, recent work on niche construction has frequently been extremely well received (Ellison 2004; Vandermeer 2004; Krakauer 2005). Rather, our aim is to make the implicit explicit, and thus facilitate a deeper understanding and appreciation of the often complex issues underlying the current debate.

SEVEN REASONS (NOT) TO NEGLECT NICHE CONSTRUCTION

1. Niche construction is not prevalent

The most direct counter to the niche-construction perspective is the argument that the impact of organisms on their environment is too weak, too transient or too capricious to significantly change selection pressures. At its extreme, we witness the position advocated by two of the founders of the modern evolutionary synthesis, George Gaylord Simpson and

Theodosius Dobzhansky, who maintained that niche-construction is primarily a human phenomenon. For instance, Simpson wrote: ''He [Man] is almost the only animal that really exerts any significant degree of control over the environment'' (Simpson 1949, p. 285). A few years later, Dobzhansky added

> ''Man alone adapts himself, in a large part, by actively or even deliberately changing the environment, and by inventing and creating new environments'' (Dobzhansky 1955, p. 339).

Simpson and Dobzhansky wrote some 50 years ago, and much has been discovered in the intervening period. As a consequence, this is the least tenable of all sceptical positions. It is well established that a vast array of organisms, from bacteria to humans, repeatedly and consistently alter their selective environments, and those of their descendants, with impacts ranging from the extremely local to the global. Odling-Smee et al. (2003) summarize a fraction of these data. Even the prima facie more defensible position, that substantive and consequential niche construction is restricted to a small number of key ''engineers,'' such as beavers, wasps, and kelp, is countered by the widespread evidence for niche construction and its consequences (Lewontin 1982, 1983, 2000; Hansell 1984, 2000, 2004; Jones and Lawton 1994, 1997; Turner 2000; Odling-Smee et al. 2003).

Even if we construe niche construction narrowly, as ''the adaptive modification by an agent of its environment,'' it remains a pervasive feature of the biological world. A brief look at the extent of niche construction in animals is sufficient to make this point. Animals construct nests, burrows, and pupal cases, provision nursery environments for their offspring, and much more. The existence of these processes is, of course, no surprise to the professional biologist, but the number and range of species involved is astonishing. For instance, there are some 9500 known species of ants and 2000 known species of termites, almost all building some kind of nest. These change the mineral and organic composition of the surrounding soil, alter local hydrology; they enable these organisms to regulate temperature, humidity, and gas exchange, and to consume vast amounts of terrestrial litter (Holldobler and Wilson 1994; Pearce 1997). There are 20,000 species of solitary bees, with immensely varied nests, and many social bees construct nests too (Gullan and Cranston 1994). There are more than 7000 species of caddis fly (Trichoptera), most of whose larvae use their silk, vegetation, and stones to build fixed or portable shelters thereby defending themselves (Hansell 1984; Gullan and Cranston 1994). Eighteen hundred species of earwigs (Dermaptera) build nests (Gullan and Cranston 1994). There are 140,000 described species of butterflies and moths, most of which construct a pupal cocoon (Gullan and Cranston 1994). Almost all of the 34,000 or more species of spiders construct a silk shelter or sac to enclose and protect their eggs, while those that do not spin webs commonly dig burrows or make nests (Preston-Mafham and Preston-Mafham 1996).

Among vertebrates there are more than 9000 species of birds, the vast majority of which construct nests (Forshaw 1998), and probably as many species of fish that do the same, or construct spawning sites and bowers (Paxton and Es-chmeyer 1998). Whereas the burrow complexes of land mammals such as moles and rabbits are well known, the burrowing behavior of the 156 species of caecilians (Order Gymnophiona), the 234 species of wormsnakes (Anomalepididae, Typhlopidae, and Leptotyphlopidae), the 900 species of gecko (Eublepharidaer and Gekkonidae), and the 1300 species of skinks (Scincidae) is less familiar. There are 135 species of chameleons that bury their eggs in simple nests, whereas all of the 250 species of turtles, terapins, and tortoises (Testudinata) construct a nest chamber. The ubiquity and impact of niche construction is no longer open to question.

2. The niche-construction perspective is not tractable

The evolutionary credentials of niche construction hang primarily on the fact that organisms regularly modify both biotic and abiotic sources of natural selection in their environments, thereby generating feedback in evolution. Yet evolutionary processes are appallingly complex, and they cannot be studied without making some simplifying assumptions. Is the feedback generated by niche construction one complication too many, as implied by Dawkins (2004)? Niche construction is undeniably a feature of the biological world, but perhaps one we cannot productively take into account in explicit analyses of evolutionary processes. If niche construction is going to pay its way as a scientific construct, it must stimulate useful empirical and theoretical work.

Odling-Smee et al. (2003) were at pains to change this perception, devoting three chapters of their book to cataloging empirical methods for testing hypotheses derived from niche-construction analysis. For instance, evolutionary biologists can use modern genomics, proteomics, or experimental evolution techniques to track the evolutionary consequences of niche construction in micro-organisms; whereas ecologists can make novel predictions about which species will invade a community, and whether the invasion will be benign or malign, based on the invader's tolerance of residents' niche construction, and the nature of the invader's activities. Other methods include experiments that investigate the consequences of canceling or enhancing a population's capacity for niche construction, comparative analyses that explore the phylogeny of trait evolution across related species (i.e., using the comparative method to detect the dependence of the evolution of recipient traits on the prior evolution of niche-constructing trait, Schwilk and Ackerly 2001), and methods for detecting the evolutionary consequences of niche construction in the wild (further details of these and other methods can be found in Odling-Smee et al. 2003).

Given the aforementioned concern with rendering evolutionary analyses tractable and productive, it is no surprise that the feedback loop from modified selective environment to the modifying organisms is rarely considered in evolutionary analyses. However, over the last few years a body of population genetics theory has accumulated that has revealed that feedback from niche construction can make a considerable difference to the evolutionary process. Incorporating niche construction into explicit analyses of evolutionary change is proving possible. Laland et al. (1996, 1999, 2001; Odling-Smee et al. 2003) have explored the dynamics of the

joint evolution of environment-altering, niche-constructing traits in organisms, and ''recipient traits,'' whose fitness depends on feedback from natural selection in environments that can be altered by niche construction. Although the results are based on specialized two-locus models, they are consistent with those of related theoretical analyses that employ other mathematical methods, such as quantitative genetic analyses of maternal inheritance and indirect genetic effects (Kirkpatrick and Lande 1989; Mousseau and Fox 1998a,b; Wolf et al. 1998, 2000).

The analyses suggest that the effects of niche construction can override external sources of selection to create new evolutionary trajectories, which leads to the fixation of otherwise deleterious alleles, the support of stable equilibria where none are expected, and the elimination of what would otherwise be stable polymorphisms. Even niche construction that only weakly affects resource dynamics, can significantly alter both ecological and evolutionary patterns. This is because traits whose fitness depends on alterable sources of selection coevolve with traits that alter sources of selection. Such coevolution results in evolutionary dynamics for both traits that are very different from what would occur if each trait had evolved in isolation. Frequently, 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 time lags in response to selection of the recipient trait, momentum effects (populations continuing to evolve in the same direction after selection has stopped or reversed), inertia effects (no noticeable evolutionary response to selection for a number of generations), opposite responses to selection, and sudden catastrophic responses to selection (Feldman and Cavalli-Sforza 1976; Kirkpatrick and Lande 1989; Laland et al. 1996, 1999, 2001; Robertson 1991; Wolf et al. 1998, 2000).

Consider a situation in which niche construction injects resources into an environment over many generations, changing the selection acting on another locus, perhaps even in another population. For instance, earthworms process soil and line burrows over multiple generations, and these activities affect the amount of topsoil and levels of soil nutrients (Satchell 1983; Lee 1985). The quantity of these constructed resources then modifies selection on alleles that influence those aspects of the earthworm phenotype affected by soil conditions, such as the structure of the epidermis and the amount of mucous secreted. Aphids and their endosymbiont *Buchnera* provide a multispecies example: The aphids affect their host plants in such a way that they produce more cystein in the phloem sap, a resource the aphids cannot produce themselves. Elevated production of plant cystein, in turn, seemingly meant that the gene for making cystein in *Buchnera* was not under strong selective constraint, and could accumulate nonsense mutations that render it disfunctional (Sandström et al. 2000; Klasson and Andersson 2004). Laland et al. (1996) found that under such conditions a time lag is generated between the change in frequency of alleles at the first locus, and the response to selection at the second locus, with two interesting consequences. First, when selection at the loci influencing niche construction stops or reverses, the

resource in the environment continues to accumulate for a number of generations, and consequently alleles sensitive to levels of the resource continue to change frequencies in the original direction (evolutionary momentum). Second, once a population reaches a stable equilibrium, it takes a greater period of time, or unusually strong selection, for the population to move away from it (evolutionary inertia).

Several recent theoretical studies corroborate and extend these findings. For instance, Hui et al. (2004) observed that niche construction profoundly influenced the dynamics, competition, and diversity of metapopulations. Silver and Di Paolo (2005) report how niche-construction traits can drive themselves to fixation by simultaneously generating selection that favors ''recipient'' trait alleles and linkage disequilibrium between niche-construction and recipient trait alleles. Kerr et al. (1999) showed how the magnitude of the tree's impact on the flammable character of the environment affected the evolution of flammability and resistance to fire in resprouting plants.

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

In summary, there is now strong theoretical and empirical support for the argument that niche construction affects the process of evolution. Such studies refute the charge that niche construction can be neglected because it is intractably complex. They also negate any suggestion that niche construction is not evolutionarily consequential. Ultimately, the fate of the niche-construction school will be decided by whether this perspective is productive. Nonetheless, there are signs that a diverse group of researchers, including evolutionary biologists, ecologists, philosophers, archaeologists, anthropologists, psychologists, and primatologists, are starting to use niche construction (Kerr et al. 1999; Schwilk and Ackerly 2001; Sole et al. 2002; Ihara and Feldman 2004; Ne'eman et al. 2004; Williams 2004). There are also several other topics outside of evolutionary biology where researchers have started to use the evolutionary framework provided by niche

construction, including new explanations for the demographic transition (Ihara and Feldman 2004; Borenstein et al. 2006), primate social behavior and social complexity (Fragaszy and Visalberghi 2001; Fragaszy and Perry 2003; Flack et al. 2006), and evolutionary theories of human behavior, language, and cognition (Mameli 2001; Sterelny 2003; Cowley 2004; Laland and Brown 2006). Perhaps the most sustained work of this kind is in ecology, where it is discussed under the term *ecosystem engineering* (Jones et al. 1994, 1997; Jones and Lawton 1995; Gurney and Lawton 1996). Ecologists are increasingly stressing the capability of organisms to modify resource flows, in the process creating and destroying habitat for other species. There is currently some optimism that this new ''engineering'' perspective may help facilitate greater integration of the various subdisciplines within ecology (Jones and Lawton 1995; Odling-Smee et al. 2003), as well as shed light on longstanding problems within ecology, such as the relationship between species richness and community stability, the factors that control ecosystem resistance and resilience, and strategies for the preservation of biodiversity (Jones and Lawton 1995; Boogert et al. 2006). This research lends credence to our view that a fruitful and productive empirical science of niche construction is indeed feasible.

3. Niche construction is not a process

A third counter-argument is that niche construction is better regarded as a background condition than an evolutionary process. There are many factors that influence evolutionary outcomes and not all are recognized as evolutionary processes. That is obviously true of abiotic factors (e.g., bolide impacts) but it is also true of biological conditions. Population size, for example, influences evolution by affecting rates of genetic drift, but few researchers would regard it as an evolutionary process in its own right. Niche construction, the suggestion goes, is like this. The effects of organisms on their environment are important to evolution without being an evolutionary process themselves (e.g., Dickins 2005). Although this argument is rarely made explicit in the published literature, it is clearly implicit in much contemporary evolutionary thought and comes up a lot in verbal discussion.

The problem with regarding niche construction as a background condition is that it conflates features of our models of evolutionary processes with those processes themselves. The distinction between a fixed background condition and an evolutionary process is relative to models of specific phenomena. If we are trying to model the evolution of rabbit resistance to calicivirus, fundamental features of rabbit breeding systems (e.g., the fact that they live and breed in warrens) are fixed background conditions. Breeding system, mutation rate, the subdivision of the population are fixed; resistance is labile. But this distinction is relative to the process we are modeling. If instead we are modeling the evolutionary diversification of the lagomorphs, that breeding system is not a fixed background condition: hares do not breed in warrens.

The same is true of niche-construction effects. If, for example, we are modeling the response of small marsupials to the invasion of foxes, we can treat the niche construction of eucalypts as a fixed background condition: their fire-starting ways tend to create open woodlands without much dense ground cover. If we are trying to model the response of eucalypts to the browning of Australia, these environmental effects are far from being a fixed background. In short, the distinction between background and process is a heuristic decision made with respect to a specific question. So this reason to exclude niche construction from evolutionary models would be justified only if it were always a good heuristic to treat niche construction effects as part of a fixed background, and that is not so.

In fact, some evolutionary biologists use the term ''process'' broadly to refer to any causal factors that play a role in evolution. In his seminal review, Endler (1986, p. 240–242) identified 21 such ''evolutionary processes,'' including ''processes which generate variation'' (e.g., DNA base substitutions, structural rearrangements, deletions, insertions, transpositions, hybridization), ''processes which restrict the kinds of variation which are either possible or likely'' (e.g., gene conversion, self regulation, constraints on development), ''processes which change frequencies of variants'' (e.g., natural and sexual selection, genetic drift), ''processes which improve an organism's fit with its environment'' (e.g., adaptation by natural selection, correlated selection), and ''processes which affect the rate or direction of evolution'' (e.g., sex, recombination, effective population size, dispersal distance). Although niche construction is absent from his list, Endler stresses the list's provisional nature and the patchiness of the knowledge on which it is based. We suggest that niche construction meets Endler's (1986) criteria for inclusion as an evolutionary process, most obviously as a factor that affects the direction of evolution.

Niche construction effects are processlike in that they are often repeated, with predictable environmental consequences. For instance, when birds build nests their consistent, directed set of behavioral actions result in a structure that is so predictable that species can be identified by their characteristic nests (Hansell 2000). Even the inadvertent production of byproducts by simple organisms, such as the manufacture of derivative chemicals by photosynthesizing cyanobacteria, are consistent, reliable, directed sets of metabolic actions that affect a change in state in the environment (here, an increase in atmospheric oxygen).

4. Niche construction is a mere effect of natural selection

Perhaps niche construction has no *independent* evolutionary significance. That would be true if niche construction effects were themselves fully explained by a preceding cause, namely as the phenotypic effects of naturally selected genes (Dawkins 2004). On the view that niche construction is a mere effect of natural selection, niche construction effects are extended phenotypes, and extended phenotypes play the same role in evolutionary biology as ordinary phenotypes, namely that of affecting the replication potential of the alleles responsible for those phenotypic effects (Dawkins 2004). Similar reasoning underlies the treatment of niche construction as an *indirect genetic effect* or IGE, with, for example, a mother's genes affecting her offspring's phenotype by modifying its environment (Wolf et al. 1998). Although this stance recognizes that modification of the selective environ-

ment occurs, contra Brodie (2005), it does not view that environmental modification as a process with quasi-independent causal significance. Rather it attributes all causal significance associated with niche-constructing activity to genes or genotypes—IGEs are, by definition, effects of genes and such genes are present because of prior selection.

This counterperspective relies on a line of analysis that, we take it, goes like this: (a) there is a direct relationship between the niche-constructing aspects of a phenotype and the naturally selected genes responsible for the development of that phenotype, and (b) because this relationship is direct, those niche-constructing effects have no independent causal significance. As we see it, both steps of this analysis fail.

(a) The relationship between genes and niche construction.—First, it is just not true that all evolutionarily consequential niche construction is under genetic control. This is well illustrated by the example of the coevolution of dairy farming and lactose absorption. Adult humans vary considerably in their ability to digest milk (Durham 1991). Consuming dairy products makes the majority of adult humans ill; the activity level of the enzyme lactase in their bodies is insufficient to break down the lactose in dairy products. Lactose tolerance depend on possession of the appropriate genes. A strong correlation exists between the incidence of the genes for lactose absorption and a history of dairy farming (Ulijaszek and Strickland 1993). This correlation has led to the hypothesis that dairy farming created the selection pressures that lead genes for lactose absorption to become common in pastoralist communities.

Following work by Aoki (1986), Feldman and Cavalli-Sforza (1989) used gene-culture coevolutionary models to investigate this possibility. Their analysis showed that the allele allowing adult milk digestion achieved a high frequency only if cultural transmission is reliable: that is, on the probability that the children of dairy-product users themselves became milk consumers. If this probability was very high then the fitness advantage of lactose absorption resulted in the selection of the absorption allele to high frequency within the 6000 years, or 300 generations available. However, if a significant proportion of the offspring of milk users did not exploit dairy products then the genes for lactose absorption would not spread. In other words, differences in the strength of cultural transmission between human societies probably account for genetic variability in lactose absorption. The analysis is able to explain both the spread of lactose absorption and the culturally related variability in its incidence. Recently, Feldman and Cavalli-Sforza's conclusions have received support from a comparative statistical analysis by Holden and Mace (1997), which concluded that dairy farming spread *prior* to the genes for lactose absorption, not the other way around. Dairy farming is an instance of human niche construction that results from human cultural processes. There are no ''genes for'' dairy farming (sensu Dawkins 1976), and it is not an adaptation (sensu Williams 1966). The difference between the cultures that farm cattle and those that do not are not explained by genetic differences between the two types of populations. In this example, niche construction is not reducible to the prior natural selection of genes controlling niche-constructing behavior, yet this activity has generated stable selection favoring genes for lactose absorption.

The lactose absorption case provides a particularly clear demonstration of the logical distinction between niche construction and natural selection, but it is far from an isolated example (Odling-Smee et al. 2003). There are almost certainly many human genes that have been selected as a direct result of human cultural niche construction, particularly activities that facilitate the spread of diseases, including sickle cell *S* allele, G6PD, TNFSF5, CCR5, AGT, CYP3A, and alleles coding for hemoglobin C and Duffly blood groups (Balter 2005). Thus, human cultural niche construction must be recognized as a significant cause of human evolution.

At first sight, it is the ''uniquely human'' capacity for culture that allows for directed, selection-generating gene-changing niche-constructing activity that is both stably inherited and not under genetic control. But cultural inheritance is likely to be characteristic of many species. If paleoanthropological evidence of culture in all species in the genus *Homo* is reliable, cultural niche construction is a major factor in hominin evolution. If primatologists are correct in their claim that geographical variation in tool use and other behavior patterns reflects cultural processes (Whiten et al. 1999; van Schaik 2003), cultural niche construction may be a factor in primate evolution. Hundreds of species of mammals, birds, and fishes are now known to learn socially (Zentall and Galef 1988; Heyes and Galef 1996). Because cultural inheritance is based on this capacity, the generality of niche construction's causal role is potentially further expanded.

Moreover, there are grounds for maintaining that niche construction reliant on entirely *asocial* learning is sufficient to modify selection pressures. The Galapagos woodpecker finch provides an example (Odling-Smee et al. 2003). These birds create a woodpecker-like niche by learning to use a cactus spine or similar implement to peck for insects under bark (Tebbich et al. 2001). Whereas true woodpeckers' (Picidae) bills are adaptive traits fashioned by natural selection for grubbing, the finch's capacity to use spines to grub for insects is not an adaptation. Rather, the finch, like countless other species, exploits a more general and flexible adaptation, namely the capacity to learn, to develop the skills necessary to grub in environments reliably containing cactus spines and similar implements. The finch's use of spines develops reliably as a consequence of its ability to interact with the environment in a manner that allows it to benefit from its own experience, but is not guaranteed by the presence of naturally selected genes, nor dependent on social learning (Tebbich et al. 2001). Moreover, the finch's 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. Although the information acquired by individuals through ontogenetic processes cannot be inherited because it is lost when they die, processes such as learning can nonetheless still be of considerable importance to subsequent generations because learned knowledge can guide niche construction, which modifies selection. If the environmental conditions that support asocial learning are stable enough, asocial learning, like the cultural transmission of dairy farming, can have a consistent effect on selection on other aspects of phe-

notype. More generally, any mechanism of phenotypic plasticity in conjunction with reliably present signals from the environment can generate the same niche-constructing activity generation by generation, with evolutionary consequences, without that activity itself being an adaptation, or precisely specified by genes, and without there necessarily being any tight correspondence between genetic and phenotypic variation (Via et al. 1995; West-Eberhard 2003; Rice 2004).

(b) Reciprocal causation.—Moreover, even if it were the case that the niche-constructing activities of organisms were under genetic control, it would not follow that niche construction was a mere effect of the prior selection of these controlling genes. For in many cases these ''controlling genes'' have themselves been selected as a result of prior niche-constructed changes in the selective environment. At issue here is the legitimacy of ''cyclical causation'' in evolutionary explanations. (Arguably, the phrase ''cyclical causation'' is not a good term to capture the causal interplay of natural selection and niche construction because, unlike say, homeostatic mechanisms in metabolism, evolving systems do not return to their original state. ''Reciprocal causation'' might be a more appropriate phrase.) Dawkins (2004) is a sceptic:

> 'Cyclical causation' leaves me cold. I must, however, make very clear that I mean causation statistically. Experimentally induced changes in bodies are never correlated with changes in genes, but changes in genes (mutations) are sometimes correlated with changes in bodies (and all evolution is the consequence). Of course most mutations occur naturally rather than experimentally, but (because correlation can't establish causation) I need to focus on 'experimentally induced' in order to pin down the direction of the causal arrow. It is in this statistical sense that development's arrow goes only one way.

Changes in bodies may not be correlated with changes in genes, but that is not true of organism-induced changes in selective environments. Provided organisms consistently and repeatedly modify their local environments, consistently and repeatedly changing selection pressures acting back on the population over significant periods of time, and consistently acting in ways that lead to the selection of certain genes as opposed to their alleles, then niche-constructing activities and niche-constructed environments will be correlated with changes in those genes, and will be the cause of those changes. If there were no correlation between niche-constructing activities and environmental states, there could be no extended phenotypes. If there were no correlation between those environmental states that are sources of selection and (recipient) genes, there would be no directional selection. Provided niche-constructing by-products are consistently generated, modify selection pressures, and precipitate a genetic response, niche changing will be correlated with, and prior to, genetic change.

This view that selection is the creative agent in evolution has often been criticized on the putative grounds that selection can only change the frequency of a trait in a population, it can never explain the existence of a trait (Sober 1984). For new traits depend on the appearance of new genetic variants, and selection never causes specific mutations. So although,

it is argued, selection can explain why a melanistic trait offering camouflage goes to fixation in a population, it cannot explain the origin of camouflage. We do not accept this line of argument, nor, we suspect, would many evolutionary biologists. It overlooks the cumulative nature of adaptive evolution. The point is most easily illustrated through a hypothetical example. Suppose that the evolution of a camouflaged bittern from a white ancestor involves some sequence of genetic changes thus:

$$G \Rightarrow G^* \Rightarrow G^{**} \Rightarrow G^{***}$$

G* appears by chance: selection does not explain its coming into existence. But by making G* more frequent in the population, selection makes the transition to G** much more likely, because it is only one mutational step away from G*, and the number of opportunities for making that step is now large, thanks to selective amplification of G*. The same process iterates. Thus, selection does explain the existence of traits, not just their prevalence in the population.

Crucially, this form of reasoning applies equally in the case of feedback on gene pools from previous niche-constructing effects. Those too are cumulative (Odling-Smee et al. 2003). For example, many bird's nests are complexly structured and often camouflaged on the outside and lined with warm materials within, having evolved through a sequence of small changes (Crook 1963; Winkler and Sheldon 1993; Hansell 2000). In fishes too, nest structures and associated nest-show displays have evolved incrementally (McLennon et al. 1988). Each of these changes resulted in new selective pressures, which changed the relative frequency of genes in the nest-building population, making some further genetic changes more likely, including in traits not directly connected to nest building, such as mating rituals, colonial living, and brain size (Crook 1963; McLennon et al. 1988; Madden 2001). Those further genetic changes enabled the process to iterate, as they resulted in new environmental conditions with downstream genetic consequences. It is true that there is a sense in which niche construction does not directly cause genetic-evolutionary events in an evolving lineage; they only facilitate their arrival. But in that same sense, selection does not explain bat echolocation. If evolutionary biologists accept that selection explains phenotypic traits, they should not resist the idea that niche construction has selection-mediated phenotypic effects.

5. *Niche construction does not change our understanding of evolution in any fundamental way*

We think that niche construction involves three changes to the way evolutionary theory is standardly depicted.

The first claim is that it introduces a second general form of inheritance. Some organism-driven changes in the environment persist as a legacy to modify selection on subsequent generations—an ''ecological inheritance'' (Odling-Smee 1988). Conventional evolutionary theory places primary emphasis on the inheritance of genes, although maternal inheritance is now recognized to be extremely widespread (Mousseau and Fox 1998a,b; Wade 1998). In contrast, the niche-construction perspective stresses two legacies that organisms inherit from their ancestors, genes and a modified environ-

ment with its associated modified selection pressures, as organisms change not only their own environment but also that of subsequent generations. It is true that ecological inheritance is not a high-fidelity template copying system: in that respect it is unlike genetic inheritance (Sterelny 2001, 2005; Dawkins 2004). But organisms transmit to their offspring altered physical and selective environments, both by physical action on their biological and nonbiological environments and by habitat choice: they affect their offspring's lives by choosing where they will live and breed, and what resources will be at their disposal. It is this ecological inheritance that generates the unusual evolutionary dynamics referred to above. Odling-Smee et al. (2003) catalog extensive examples of ecological inheritance.

Second, niche construction modifies not just selective environments but developmental environments. In addition to generating an ecological inheritance, niche construction modulates genetic inheritance. Systematic changes in the developmental environment will result in systematic changes to the phenotypic expression of inherited genes. Sometimes niche construction will modify the shape of the relevant norm of reaction, for example, by reducing the range of developmental environments to which juveniles are exposed. Nests, burrows, mounds, and similar structures all tend to buffer environmental variation, making temperature, humidity, and exposure to wind and sunlight more uniform. If, in a seabird lineage, there is an evolutionary trajectory from ground to burrow nesting, a host of adaptations of egg and juvenile will no longer be relevant: for example, there is no need for camouflaged eggs. But the developmental environment will also become more uniform. So alleles that have equivalent phenotypic effects in burrow-rearing environments but not in a broader class of environments will become selectively equivalent. But an allele that is fitter in this narrower class of environments will have its advantage magnified, because this will have become the typical rather than the occasional environment in which genes are expressed. The heritability of the trait associated with such an allele would also be affected by this reduction in environmental variation. Conversely, niche construction can sometimes result in exposure to a broader range of developmental conditions. For example, when parents relocate, their offspring are exposed to novel developmental as well as selective environments. In both circumstances, the constructed environment is not only a modified source of selection but also a determinant of the range of phenotypes exposed to selection. The modification of reaction norms through the construction of developmental environments potentially influences the heritability and response to selection of plastic traits, in some cases exposing genetic variation to selection, in other cases shielding it from selection. Similar arguments have been made with respect to phenotypic plasticity (West-Eberhard 2003). Examples of such phenomena can be found in West-Eberhard (2003) and Donohue (2005).

The third claim is that acquired characteristics, for instance, dairy farming or woodpecker finch tool use, influence the selective environment. Through that influence, such acquired characters play a role in the evolutionary process through the thoroughly Darwinian process of natural selection. In invertebrates, a role for acquired characteristics in evolution is already recognized, particularly habitat imprinting (Jaenike 1982). However, this role is not solely dependent on learning. For instance, corals influence water speeds, the erosive impact of waves, siltation rates, and so forth (Jones et al. 1994), an instance of niche construction, but their capacity to do so is in itself affected by water flow.

Acquired characteristics are of particular significance to vertebrate evolution. There is already considerable interest among evolutionary biologists in the role that imprinting, song learning, habitat imprinting, cultural transmission, and various other forms of learning play in speciation, the evolution of adaptive specializations, adaptive radiations, the colonization of new habitats, brood parasitism, and sexual selection in vertebrates (ten Cate and Bateson 1988; Kirkpatrick and Dugatkin 1994; Laland 1994; ten Cate 2000; Aoki et al. 2001; Beltman et al. 2003, 2004; West-Eberhard 2003).

The significance of acquired characters to evolutionary processes becomes amplified with stable transgenerational culture, and it is now widely believed that such characters were probably extremely important to hominid evolution (Richerson and Boyd 2004). For instance, theoretical analyses by Laland et al. (2001) explored the evolutionary consequences of cultural niche construction. They revealed circumstances under which cultural transmission could overwhelm natural selection, accelerate the rate at which a favored allele spreads, initiate novel evolutionary events, and possibly trigger hominid speciation. In fact, the analysis found that, because cultural processes typically operate faster than natural selection, cultural niche construction is likely to have more profound consequences than gene-based niche construction.

6. Niche construction does not bring about adaptation

One fundamental aspect of nature that evolutionary theory sets out to account for is the "hand-in-glove" fit of living organisms to their environments. The conventional perspective explains this complementarity as resulting solely from natural selection sculpting organisms to their environments. Conversely, the niche-construction perspective recognizes two logically distinct routes to an organism-environment match: natural selection (driving asymmetric accommodation to the environment) and niche construction. The latter involves the construction, depletion, modification, or regulation of resources by organisms in their environments, in a manner that enhances their fitness to the environment.

Once again earthworms provide a useful example. Earthworms are structurally very poorly adapted to cope with physiological problems such as water and salt balance on land, and they would seem to belong in a freshwater habitat (Turner 2000). For instance, they produce the high volumes of urine characteristic of freshwater rather than terrestrial animals. That is because earthworms have retained their ancestral freshwater kidneys (or nephridia) and have evolved few of the structural adaptations one would expect to see in an animal living on land. They can only survive in a terrestrial environment by coopting the soils that they inhabit and the tunnels they build to serve as accessory kidneys that compensate for their poor structural adaptation (Satchell 1983; Lee 1985; Turner 2000). These originally aquatic creatures

are able to solve water- and salt-balance problems through their niche construction, by tunneling, exuding mucus, eliminating calcite, etc. By producing well-aggregated soils, the worms weaken matric potentials and make it easier for them to draw water into their bodies (Turner 2000). In the process, earthworms dramatically change their environments (Satchell 1983; Lee 1985). Through their burrowing activities, their dragging organic material into the soil, their mixing it up with inorganic material and their casting, which serves as the basis for microbial activity, earthworms dramatically change the structure and chemistry of the soils in which they live, often on a huge scale (Satchell 1983; Lee 1985).

All of this earthworm activity highlights a problem with the concept of adaptation. In this case it is the soil that does the changing, rather than the worm, to meet the demands of the worm's freshwater physiology (Turner 2000). So what is adapting to what? Standard evolutionary theory shortchanges the active role of organisms in constructing their environments, generating explanations that are sometimes incomplete and misleading. The ancestors of contemporary earthworms must have chosen and partly constructed the soil environments to which they are now adapted, because without ancestral niche construction topsoil would not exist.

There are two logically distinct routes to the complementary match between organisms and their environments. Either organisms can change to suit their environments, or environments can be changed by organisms to suit themselves. Contemporary earthworms bring about this match with their soil environment, in part, by the second route; through earthworm-induced changes in soil. On the standard perspective, this second route to the complementary match between organisms and environments is reduced to the first. We agree that the niche construction of earthworms both now and in the past has probably been influenced by natural selection acting on genes favoring earthworm niche-constructing activities. Thus, the earthworm and its soil is qualitatively different from the match between dairy farming and lactose absorption. As dairy farming is not under genetic control, there is no question of reducing this complementary match to the natural selection of farming genes. Even so, the activity of the earthworm is not well handled by the standard perspective. The extended phenotype model is not a good account of the relationship between earthworms and soil, because some aspects of worm niche construction are probably not adaptations. Moreover, unlike nests and burrows, the worm-friendly soil is a collective rather than individual product. What is more, there is no obvious boundary between the worm-adapted zones of the soil, and the worm-unfriendly zones. Thus, there is no well-defined extended phenotype-environment boundary.

Moreover, most biologists simply assume that the process of constructing a match began with the natural selection of new genetic variation in earthworm ancestors that allowed them to live in and partly modify soils, even if those modifications then led to the selection of further genetic changes and more extensive environmental engineering. This is possible, but so is an alternative trajectory. This worm-environment match may have first been bought about as a result of niche construction resulting from phenotypic plasticity of ancestral worms prior to selection favoring tunneling, burrow

lining, and other soil-processing adaptations. Cognitive complexity is not required for adaptive phenotypic plasticity: plants have such capacities (Donohue 2005). Anyone who doubts that earthworms possess such phenotypic plasticity would do well to consult Darwin (1881). Finally, as we have already argued in section 4, even if the current niche-constructing activities of worms are under the control of alleles selected for the task, those alleles are present in worm genotypes partly as a result of the modifications made by worms of earlier soils. They have been selected through agent-caused changes in ancestral environments.

In summary, if ''adaptation'' means the asymmetric accommodation of a lineage to its environment, then niche construction does not cause adaptations (sensu Williams 1966) in the niche-constructing lineage. (Niche construction may cause adaptations in this sense in other lineages: domestic mice are adapted to human-caused changes in their environment.) But although niche construction may not explain adaptations in this narrow sense, it does explain organism-environment matches.

7. Niche construction is not a unified phenomenon

In their 2003 monograph, Odling-Smee et al. defined niche construction very broadly, as any impact by an organism on its selective environment. So defined, niche construction is often of negligible importance: many impacts are unsystematic and transient. Moreover, it is often negative: organisms degrade their local environments as they extract resources and add wastes. But if niche construction is taken as any change that organisms bring about in selective environments, it is necessarily universal. For metabolism is essential to life (Maynard Smith and Szathmary (1995, p. 17), and as all metabolism brings about chemical changes in the local environment, it follows that niche construction is universal. Moreover, the universality of niche construction can be derived from a consideration of some basics of thermodynamics (Laland et al. 2005). Work, in the thermodynamic sense, is done when energy is made to flow. Organisms engage in work, because they need to exchange energy with their environments, to channel energy through their bodies, and to create orderliness in their bodies and their immediate surroundings. Work is a necessary condition for organisms to survive and maintain their ''far-from-equilibrium'' status against entropic forces. Organisms feed on molecules rich in free energy, in the process generating outputs largely in the form of molecules poorer in free energy. To survive, organisms must act on their environments and in doing so they must change them.

The utility of the niche-construction concept is not compromised by universality. Metabolism, homeostasis, growth, selection, are all universal features of living creatures that earn their keep as scientific concepts. Although it is not interesting or surprising to claim that a particular creature constructs its niche, it is of interest if this construction affects evolutionary and coevolutionary dynamics.

Nonetheless, a broad definition of niche construction has been criticized (Dawkins 2004; Okasha 2005; Sterelny 2001, 2005; Griffiths 2005; Brodie 2005). For instance, Sterelny (2001, p. 333) notes:

''Some of these impacts are mere effects; they are by-products of the organism's way of life. But sometimes we should see the impact of organism on environment as the organism *engineering* its own environment: the environment is altered in ways that are adaptive for the engineering organism.''

Dawkins (2004) draws on the same distinction to argue that the term ''niche construction'' should be restricted to extended phenotypes, that is, to adaptations, and that an alternative term adopted for niche-modifying by-products:

''Niche construction is a suitable name only for the second of these two (and it is a special case of the extended phenotype). There is a temptation, which I regard as little short of pernicious, to invoke it for the first (byproducts) as well. Let's call the first type by the more neutral term, ''niche changing,'' with none of the adaptive implications of niche construction.''

This argument has been elaborated by Brodie (2005), who maintains that niche-constructing adaptations and by-products will generate different kinds of dynamics. This argument might be important in some contexts, but it is not important to this paper. For in the first six sections of this paper, we have largely restricted ourselves to the narrower sense: the sense in which organisms engineer environments to their own benefit. Even if the term ''niche construction'' is restricted to extended-phenotype-like adaptations, and all cases of ''niche-changing'' are dismissed completely, niche construction is widespread and evolutionarily consequential. Organisms' activities frequently modify selection pressures acting on other aspects of the phenotype, in the same or in descendant populations. Moreover, they have other evolutionarily significant effects; for example, they affect the expression of genetic and phenotypic variation.

Importantly, these evolutionary ramifications remain whether or not the subsequent evolution of niche-constructing adaptations differs qualitatively from that of niche changing (or niche-constructing by-products). When earthworms change soil chemistry they modify selection pressures as surely as when they line their burrows with leaves, despite the fact that probably only the latter instance can be described as an adaptation. If critics of the niche-construction perspective describe niche-constructing by-products as ''mere effects'' to disregard them, this in itself is a powerful argument for maintaining a broad definition of niche construction.

A related argument is that it may not be *useful* to treat niche construction as a unitary phenomenon (Keller 2003; Manning and Godfray 2004). Evolutionary biologists and ecologists have devised means for dealing with the feedback generated by niche construction within the framework of standard evolutionary theory. These include models of (1) ecological and demographic processes (e.g. resource depletion), (2) frequency- and density-dependent selection, (3) habitat selection, (4) coevolution, (5) maternal inheritance and maternal effects, (6) epistasis and indirect genetic effects, (7) gene-culture co-evolution, and (8) evolution in spatially heterogeneous environments, reviewed in Odling-Smee et al. (2003).

These theoretical developments are important. They explain some of the phenomena central to the niche-construction perspective, and illustrate the fact that niche construction is far from being entirely neglected by evolutionary biologists. However, even collectively, these bodies of theory continue to understate the importance and pervasiveness of niche construction. Niche construction often remains unrecognized as an evolutionary cause, and certain forms of selective feedback remain understudied. As sketched in section 2, one practical advantage of treating niche construction as a unitary phenomenon is that it brings with it a fresh perspective, novel hypotheses, and new methods that can stimulate research within evolutionary biology. A unitary perspective sharpens evolutionary biology's search image. The selfish gene perspective proved valuable by foregrounding conflicts of interest within organisms, between the sexes, and between generations. Likewise, the niche-construction perspective foregrounds the impact of organisms on selective environments.

In summary, there is overwhelming evidence that niche construction is ubiquitous and that it generates stable and consistent modifications in selection pressures. This conclusion holds independently of definitions of niche construction. There is both accuracy and utility in treating niche construction as a unitary phenomenon.

Concluding Remarks

This paper develops a case for four claims. First, minimally, intervention by organisms in their environment, especially their physical environment, is a substantially understudied domain of evolutionary biology. Second, the niche-construction perspective is heuristically valuable: it draws our attention to a range of phenomena that are both important and easily to overlook on standard perspectives. Third, convincing theoretical and empirical evidence supports the argument that niche construction should be regarded as an evolutionary process. Fourth, the standard unidirectional explanation of the impressive ''fit'' between organisms and their environments in terms of a one-way accommodation of organisms to their environment leaves out an important part of its evolutionary cause, namely, niche construction. We hope that this article will stimulate other researchers to recognize the evolutionary credentials of niche construction, and encourage the many evolutionary biologists who currently study niche construction, often under another name, to view their work as part of a new and valuable general framework within evolutionary biology.

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