

CHAPTER 1

Introduction

To see what is in front of one's nose requires
a constant struggle.
(George Orwell)

Organisms play two roles in evolution. The first consists of carrying genes; organisms survive and reproduce according to chance and natural selection pressures in their environments. This role is the basis for most evolutionary theory, it has been subject to intense qualitative and quantitative investigation, and it is reasonably well understood. However, organisms also interact with environments, take energy and resources from environments, make micro- and macrohabitat choices with respect to environments, construct artifacts, emit detritus and die in environments, and by doing all these things, modify at least some of the natural selection pressures present in their own, and in each other's, local environments. This second role for phenotypes in evolution is not well described or well understood by evolutionary biologists and has not been subject to a great deal of investigation. We call it "niche construction" (Odling-Smee 1988) and it is the subject of this book.

All living creatures, through their metabolism, their activities, and their choices, partly create and partly destroy their own niches, on scales ranging from the extremely local to the global. Organisms choose habitats and resources, construct aspects of their environments such as nests, holes, burrows, webs, pupal cases, and a chemical milieu, and frequently choose, protect, and provision nursery environments for their offspring. Niche construction is a strongly intuitive concept. It is far more obvious than natural selection because it is far easier to observe individual organisms *doing* niche construction than to observe them *being* affected by natural selection. It is self-evident that all organisms must interact with their environ-

ments to stay alive, and equally obvious that, when they do, it is not just organisms that are likely to be affected by the consequences of these interactions, but also environments. That organisms actively contribute toward both the “construction” and “destruction” of their own and each other’s niches is scarcely news. So why write a book about it?

The answer is that, when subject to close scrutiny, it becomes clear that niche construction has a number of important, but hitherto neglected implications for evolutionary biology and related disciplines. In fact, in this book we go so far as to argue that niche construction changes our conception of the evolutionary process. Niche construction should be regarded, after natural selection, as a second major participant in evolution. Rather than acting as an “enforcer” of natural selection through the standard physically static elements of, for example, temperature, humidity, or salinity, because of the actions of organisms, the environment will be viewed here as changing and coevolving with the organisms on which it acts selectively.

Using a combination of empirical data, comparative argument, and mathematical modeling we will try to convince the reader of the merits of this new way of thinking about evolution. We will illustrate how niche construction can change the direction, rate, and dynamics of the evolutionary process. Niche construction is a potent evolutionary agent because it introduces feedback into the evolutionary dynamic. Niche construction by organisms significantly modifies the selection pressures acting on them, on their descendants, and on unrelated populations. The later chapters of this book describe how niche construction can be incorporated into empirical and theoretical evolutionary analyses, and how it can be used to generate hypotheses. We will present methods for testing these hypotheses and point to the broad areas of biology and the social sciences to which they are applicable. Our hope is that the niche-construction perspective will prove fruitful by leading to the development of testable new theories and facilitating greater understanding of the evolutionary process.

In this first chapter we introduce the concept of niche construction, and spell out its major consequences with illustrative examples from natural history. We describe four major ramifications of niche construction. Niche construction may (1) in part, control the flow of

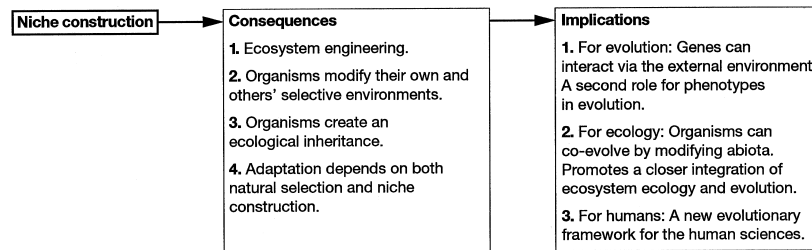


FIGURE 1.1. The consequences of niche construction and their implications for evolutionary theory, ecology, and the human sciences.

energy and matter through ecosystems (ecosystem engineering), (2) transform selective environments to generate a form of feedback that may have important evolutionary consequences, (3) create an ecological inheritance of modified selection pressures for descendant populations, and, finally (4) provide a second process capable of contributing to the dynamic adaptive match between organisms and environments (see fig. 1.1). We then consider some of the implications of these consequences for three different bodies of biological theory, namely, evolutionary theory itself, the relationship between evolutionary theory and ecosystem ecology, and the relationship between evolutionary theory and the human sciences.

1.1 THE CONSEQUENCES OF NICHE CONSTRUCTION

1.1.1 Ecosystem Engineering

We begin with an example of a potent niche constructor, the genus of leaf-cutter ants, *Atta*, as described by the myrmecologists Bert Hölldobler and Edward Wilson (1994). At present, 15 species of leaf-cutter ants are known to science. All of them live in the New World across a geographical range that stretches from the southern states of the United States of America to the south of Argentina. The most salient niche-constructing activity of this genus is “agriculture.” Leaf-cutter ants grow fungi on substrates of fresh vegetation that they initially cut and collect from outside their nests and then carry into their nests to form the basis of fungal gardens (fig. 1.2). The fungal

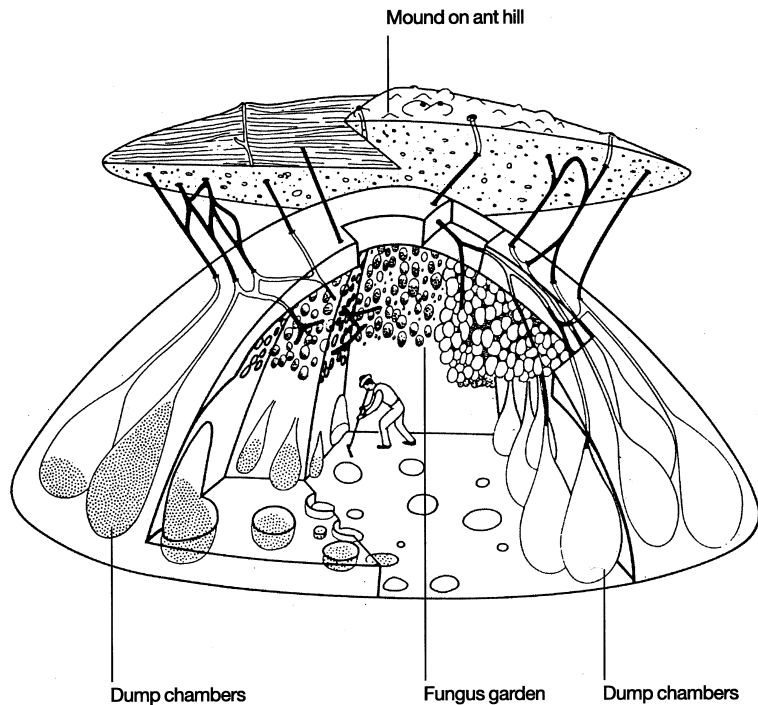


FIGURE 1.2. A giant nest built by a species of leaf-cutter ants, *Atta sexdens*, consisting of about a thousand chambers. In this particular example the nest is so huge that the loose soil brought out and piled on the ground by the ants while making it occupied more than 22 m³ and weighed approximately 44 tons. The human figure shown inside the nest indicates the scale. (Reproduced from Hölldobler and Wilson 1994. From an illustration by J.C.M. Jonkman in *Insect-Fungus Symbiosis: Mutualism and Commensalism*, edited by L. A. Batra [Montclair, NJ: Allanheld and Osman, 1979]. Modified by N. A. Weber for Hölldobler and Wilson [1995], p. 116.)

crop that the ants grow consists of a fluffy white mold, resembling bread mold, made up of masses of thread-shaped hyphae. The ants' agriculture is so efficient that it not only provides them with an abundant supply of food, but enables individual colonies to reach staggeringly large sizes, with a single colony containing millions of workers. In one extreme case described by Hölldobler and Wilson, a nest of the species *Atta sexdens* consisted of about a thousand chambers, with the chambers varying in size from that of a closed fist to

that of a soccer ball. Three hundred and ninety of its chambers were still in use when it was discovered, and they were filled with both fungal gardens and ants. This particular nest was so huge that the loose soil that had been brought out and piled on the ground by the ants in the course of making their nest occupied over 22 cubic meters and weighed approximately 40,000 kilograms, or 44 tons. Such an example makes it clear that the collective leaf-cutting activities of such large colonies of ants can have enormous impacts on the ants' surrounding environment.

Given such a prodigious capacity for niche construction, it is not surprising that several species of leaf-cutter ants, including *Atta cephalotes* and *Atta sexdens*, turn out to be among the worst pests of Central and South America. They destroy billions of dollars worth of agriculturally valuable crops each year. For instance, in Brazil, leaf-cutter ants are especially destructive in eucalyptus and citrus plantations. What is, perhaps, more surprising is that the same ants produce beneficial effects in ecosystems. For example, the ants turn over and aerate large quantities of soil in forests and grasslands, and they also circulate nutrients that are essential to the lives of many other species of organisms with whom they share their ecosystems. Moreover, it has recently been discovered that leaf-cutter ants can help the recovery of rainforests in areas where the primary forest has been destroyed by human farmers and loggers. Here, the ants' activities benefit newly established plants because the soil from their nests is much easier than the surrounding soil for young plant roots to penetrate. Also, the decomposition of the plant material that the ants store in their nests increases the soil's pH, thereby increasing its capacity to retain its nutrients, preventing them from being washed away out of reach of the plants.

Leaf-cutter ants are a good illustration of the first major consequence of niche construction. The activities of organisms can result in significant, consistent, and directed changes in their local environments. Simply by choosing or perturbing their habitats, for example, by repeatedly consuming the same resource, or repeatedly emitting the same detritus, organisms can substantially modify their worlds, and do so in a nonrandom or predictable manner. As a consequence, niche-constructing organisms frequently modify the environments of other organisms too, including organisms in other species. They also

affect some of the properties of the ecosystems that they share with other species, in ways that may either harm or benefit other organisms. For instance, as the major herbivores of the neotropics, leaf-cutter ants clearly have an impact on the growth and density of those species of plants that they exploit, as well as on those plants that grow in the improved soil of their nests and those species that rely on the ants to disperse their seeds. Moreover, leaf-cutter ants have glands that secrete substances that kill virtually all bacteria and fungi, except for the single fungus that they cultivate.

While the leaf-cutter ants provide a particularly striking example, there is nothing remarkable about the fact that they have an impact on their local ecology. In chapter 2 of this book we will demonstrate that niche construction is extremely common. Population-community ecologists know a good deal about how organisms can affect each other's environments, both inter- and intraspecifically, and how, by doing so, they can influence such phenomena as the distribution and abundance of organisms, population and community structures, food webs, and trophic dynamics (Begon et al. 1996; DeAngelis 1992; Rosenzweig 1995). Similarly, ecosystem ecologists already have a good understanding of the many ways in which organisms can influence energy and matter flows through ecosystems when they take resources from them, or return detritus to them, and also how their influence can, in turn, affect the structure and function of ecosystems, the resistance and the resilience of ecosystems to perturbations, and the nature of various biogeochemical cycles (O'Neill et al. 1986; Odum 1989; Jones and Lawton 1995; Patten and Jorgensen 1995).

For our purposes, however, a recent insight from a team of ecosystem ecologists, Jones et al. (1994, 1997) and Jones and Lawton (1995), is particularly valuable. Jones et al. describe organisms that choose or perturb their own habitats as "ecosystem engineers," where "ecosystem engineering" is essentially the same as "niche construction." Jones et al. claim that when organisms invest in ecosystem engineering they not only contribute to energy and matter flows and trophic patterns in their ecosystems but in part also *control* them. They propose that organisms achieve their control via an extra web of connectance in ecosystems, which they call an "engineering web," and which is established by the interactions of diverse species of engineering organisms (Jones et al. 1997). This engineering web op-

erates in conjunction with the familiar material (stoichiometric) and energy (thermodynamic) webs of connectance in ecosystems that are already studied by ecologists (Reiners 1986). Jones et al. also suggest that it is not always necessary for ecosystem engineers to contribute directly to a particular energy or material flow among a set of trophically connected organisms in an ecosystem for them to control the flow (Jones et al. 1997, p. 1952).

We can illustrate these ideas by using two of Jones et al.'s own examples, both taken from the Negev desert in Israel. The first is a case of engineering by microorganisms. In many deserts, including the Negev, the soil is extensively covered by dominant microphytic communities of blue-green algae, cyanobacteria, and fungi. Although these microorganisms are barely visible to the naked eye, they nevertheless have a powerful engineering effect because they secrete polysaccharides that bind the desert's soil and sand together to form a crust that not only protects their own colonies from heat, but also controls erosion, runoff, and site availability for the germination of higher plants in the desert (West 1990; Zaady and Shachak 1994; Jones et al. 1997). After rain, the asphaltlike patches that are created by these microorganisms reduce the absorption of water by about 30%, and this increases the runoff of water, allowing the water to form pools in pits previously dug, for example, by desert porcupines digging for geophytes. Windblown seeds then germinate in these moist pits and give rise to lush oases that may eventually harbor dozens of other species (Alper 1998). Yet all of this ultimately depends on the long reach of the engineering activities of microorganisms.

The second example is provided by three species of snail, *Euchondrus* spp., that eat endolithic lichens that grow under the surface of limestone rocks in the Negev desert. One consequence of this unusual form of herbivory is that the snails are major agents of rock weathering and also of soil formation in this desert. Their agency, however, is not due to the amount of lichens they consume, which is actually rather little. Instead, it is due to the unexpected fact that these snails have to physically disrupt and ingest the rock substrate in order to consume the lichens. They later excrete the rock material ingested as feces, which they deposit on the soil under the rocks. Shachak et al. (1987) estimated that the annual rate of biolog-

ical weathering of these rocks by snails is 0.7 to 1.1 metric tons per hectare per year, which is sufficient to affect the whole desert ecosystem (Shachak et al. 1987; Shachak and Jones 1995). By converting rock to soil at this rate, the snails become major agents in soil formation.

So ecosystem control is one major new idea associated with the ecological effects of niche construction. It stems from the capacity of niche-constructing organisms to modify not only their own environments but also the environments of other organisms in the context of shared ecosystems.

1.1.2 The Modification of Selection Pressures

The second consequence of niche construction, and its first evolutionary consequence, derives from these ecological effects. If organisms modify their environments, and if in addition they affect, and possibly in part control, some of the energy and matter flows in their ecosystems, then they are likely to modify some of the natural selection pressures that are present in their own local selective environments, as well as in the selective environments of other organisms. In fact, it is difficult to see how organisms can avoid doing this. Environmental change modifies natural selection pressures (Endler 1986), while organisms are a known source of environmental change in ecology (Jones et al. 1997).

However, in order for niche construction to be a significant evolutionary process, it is not sufficient for niche-constructing organisms to modify one or more natural selection pressures in their local environments temporarily, because whatever selection pressures they do modify must also persist in their modified form for long enough, and with enough local consistency, to be able to have an evolutionary effect. Often this criterion will not be met. Moreover, independent agents in a population's environment may erase or overwhelm the effects of the population's niche construction, thereby ensuring that there is no persistent environmental change caused by the population's activities. For instance, other environmental agents may disperse a population's detritus by dissipating it over time, or, if the

agents are detritivores, they may consume the population's detritus, or recycle it, instead of allowing the detritus to accumulate.

There are, however, at least two ways in which this persistence criterion can be satisfied. If, in each generation, each individual repeatedly changes its own ontogenetic environment in the same way, for instance, because each individual inherits genes that express the same niche-constructing phenotypes, then ancestral organisms may modify a source of natural selection by repetitive niche construction. The immediate environmental consequences of this kind of niche construction may be transitory, and may be restricted to single generations only, but if the same environmental change is reimposed sufficiently often and persists for a sufficient number of generations, it may modify the pressures of natural selection in local environments and therefore drive a new evolutionary episode.

For example, individual web spiders repeatedly build webs in their local environments, generation after generation, because they repeatedly inherit genes from their ancestors that are expressed in web construction. Even though spiders' webs are transitory objects, and are only too likely to be destroyed on a daily basis by other agents in the environment, such as other animals, or the weather, every time a spider's web is destroyed the spider's genes "instruct" the spider to make a new one. As a result there is almost always a web in the local environments of these spiders. The omnipresent web appears to have fed back, over many generations, in the form of modified natural selection. For instance, spiders on a web are exposed to the threat of avian predators, but they frequently engage in courtship and process prey on the web. Thus the web may have been a source of selection to favor further phenotypic changes in these species, including the marking of their webs to enhance crypsis, differential responses to the frequency of web vibration for prey and for a potential mate, or, as in the case of one genus of African orb-web spider, *Cyclosa*, the building of dummy spiders in the web probably to divert the attention of birds that prey on them (Edmunds 1974; Preston-Mafham and Preston-Mafham 1996).

The second way of satisfying the same persistence criterion occurs when all or a part of the consequences of one generation's niche-constructing activities persist in their modified form in the selective

environments of a succeeding generation. By this means, ancestral organisms can bequeath legacies of modified natural selection pressures to their descendants via the external environment. This between-generational transmittal may be restricted to just two generations, as happens, for example, in maternal inheritance (Kirkpatrick and Lande 1989; Cowley and Atchley 1992; Schluter and Gustafsson 1993; Mousseau and Fox 1998a,b) when mothers modify the selection pressures in the local environments of their offspring. Alternatively, it may be a multiple-generation phenomenon in which the cumulative effects of generations of niche construction modify the selective environments of more distant descendants.

The common cuckoo, *Cuculus canorus*, provides a familiar two-generation example. In this species of brood parasite, cuckoo mothers repeatedly select a host belonging to some other bird species and lay their eggs in the chosen host's nests, subsequently relying entirely on this host to incubate the cuckoo eggs and raise the cuckoo young to independence. Cuckoo mothers have parasitized other birds in this way for generations and, as a result, have apparently bequeathed modified natural selection pressures to their offspring, in the form of these alien nurseries. The modified natural selection pressures have probably contributed to several novel adaptations in cuckoo chicks, including an extremely short incubation period, which ensures that the cuckoo chicks usually hatch before the host's chicks, and the ejection of the host's eggs from the nest or the killing of any of the host's chicks that have managed to hatch. These latter acts are themselves further examples of niche construction, this time via the agency of the cuckoo chicks rather than their mothers. The effect is that each cuckoo chick is raised on its own by its host and does not have to compete with any rival chicks when its foster parent arrives with food. However, having killed its rivals, the cuckoo chick must stimulate an adequate rate of feeding by its host. It appears to accomplish this task by behaving as if it were the equivalent of a whole brood of its host's chicks, instead of just a singleton. It does so by emitting a rapid begging call that mimics the begging sounds, as well as the calling rate, of a complete brood of its host's chicks (Davies et al. 1998). The initial choice of host's nests by cuckoo mothers may also have made possible some additional adaptations in their offspring when the latter become parents. For example, cuckoos that

were raised in the nests of a particular host species subsequently tend to parasitize the same host species, possibly because as they developed they learned their hosts' characteristics (Krebs and Davies 1993). The mother's niche construction has modified the selection on her offspring, resulting in a cascade of evolutionary events, including the selection of further niche construction on the part of the chick. In recent years there has been increasing recognition that such maternal effects are both taxonomically widespread and evolutionarily significant (Wade 1998; Mousseau and Fox 1998a).

Earthworms provide an equally familiar multigenerational example, one which has the added distinction of having been described by Darwin (1881). 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 scale that exceeds even the soil-perturbing activities of leaf-cutter ants. For instance, in temperate grasslands earthworms can consume up to 90 tons of soil per hectare per year. Similarly, as a result of their industry, earthworms affect ecosystems by contributing to soil genesis, to the stability of soil aggregates, to soil porosity, to soil aeration, and to soil drainage. Also, because their casts contain more organic carbon, nitrogen, and polysaccharides than the parent soil, earthworms can also affect plant growth by ensuring the rapid recycling of many plant nutrients. In return, the earthworms probably benefit from the extra plant growth they induce by gaining an enhanced supply of plant litter (Kretzschmar 1983; Hayes 1983; Stout 1983; Lee 1985; Ellis and Mellor 1995). All of these effects typically depend on multiple generations of earthworm niche construction, leading only gradually to cumulative improvements in the soil. It follows that most contemporary earthworms inhabit local selective environments that have been radically altered, not just by their parent's generation, but by many generations of their niche-constructing ancestors. It is likely that some earthworm phenotypes, such as epidermis structure, or the amount of mucus secreted, coevolved with earthworm niche construction over many generations. Moreover, because these originally aquatic creatures are able to solve their water- and salt-balance problems through tunneling, exuding mucus, eliminating calcite, and dragging leaf litter

below ground, that is, through their niche construction, earthworms have retained the ancestral freshwater kidneys (or nephridia) and have evolved few of the structural adaptations one would expect to see in an animal living on land (Turner 2000). For instance, earthworms produce the high volumes of urine characteristic of freshwater rather than terrestrial animals.

The production of oxygen by photosynthetic organisms is another multiple-generation example, which illustrates the extreme effects that niche construction can have on a global scale if its consequences happen to build up over long periods of time. When photosynthesis first evolved in bacteria, particularly in cyanobacteria, a novel form of oxygen production was created. The contribution of these ancestral organisms to the earth's 21% oxygen atmosphere must have occurred over billions of years, and it must have taken innumerable generations of photosynthesizing organisms to achieve. It is highly likely that modified natural selection pressures, stemming from the earth's changed atmosphere, played an enormous role in subsequent biological evolution. For example, many organisms have evolved a capacity for aerobic respiration, and they have also evolved other mechanisms, such as the enzyme superoxide dismutase, that protect cells against oxidation (Futuyma 1998).

In the next chapter we illustrate traits in many species that appear to have evolved as a consequence of selection generated by prior niche construction. However, if organisms evolve in response to selection pressures modified by their ancestors, there is feedback in the evolutionary dynamic, and it is well established that biological systems with feedback behave quite differently from those without it (Robertson 1991). This is a further point to which we shall repeatedly return in this book.

1.1.3 Ecological Inheritance

With the exception of the special cases of maternal and cultural inheritance (reviewed in chapter 3) standard evolutionary theory is typically concerned with only a single general inheritance system in evolution. It assumes that natural selection among individual organisms influences which individuals survive and reproduce to pass on

their genes to the next generation (fig. 1.3a), and this genetic inheritance is generally regarded as the only inheritance system to play a major role in biological evolution. This assumption is not affected by niche construction as long as the physical consequences of the niche-construction process are erased in the selective environments of populations between each generation, and therefore last only a single generation. For instance, in the orb-web spider case, the repetitive construction of webs by spiders owes its capacity to influence the evolution of populations of spiders not to any between-generation persistence of the webs themselves (spiders' webs are far too transitory for that), but rather to the spider's genetic inheritance system. This ceases to be true, however, when the physical consequences of one generation's niche construction are not completely erased in the environments of its descendants but are instead bequeathed, either wholly or in part, from one generation to the next, in the form of legacies of modified natural selection pressures. This is what happens in the case of cuckoos over two generations, and in earthworms and in cyanobacteria over multiple generations. Here, then, is a third major consequence of niche construction. Where niche construction affects multiple generations, it introduces a second general inheritance system in evolution, one that works via environments. This second inheritance system has not yet been widely incorporated by evolutionary theory.

We call this second general inheritance system *ecological inheritance* (Odling-Smee 1988; Odling-Smee et al. 1996). It comprises whatever legacies of modified natural selection pressures are bequeathed by niche-constructing ancestral organisms to their descendants. Ecological inheritance differs from genetic inheritance in several important respects. First, genetic inheritance depends on the capacity of reproducing parent organisms to pass on replicas of their genes to their offspring. Ecological inheritance, however, does not depend on the presence of any environmental replicators, but merely on the persistence, between generations, of whatever physical changes are caused by ancestral organisms in the local selective environments of their descendants. Thus, ecological inheritance more closely resembles the inheritance of territory or property than it does the inheritance of genes. Although the inheritance of property is common enough among human beings, it is not restricted to humans. As

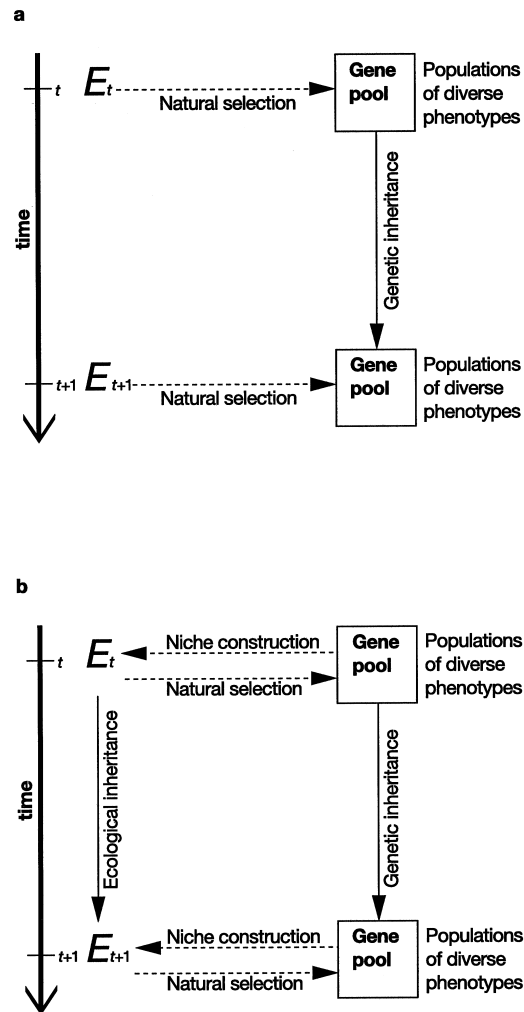


FIGURE 1.3. (a) Standard evolutionary perspective: Organisms transmit genes from generation t to generation $t + 1$ with natural selection acting on phenotypes. (b) With niche construction: Organisms also modify their local environments (E), as depicted by the arrow labeled “niche construction.” Each generation inherits from ancestral organisms both genes and a legacy of modified selection pressures, described as “ecological inheritance.” (From Laland et al. [2000b], fig. 1. Reprinted with the permission of Cambridge University Press.)

we have seen, cuckoos inherit an alien nest while earthworms inherit a modified soil environment. Ecological inheritance also has a lot in common with the more familiar concept of ecological succession, except that it has evolutionary as well as ecological consequences because it involves the inheritance by populations of modified natural selection pressures, via a succession of environmental states, which may then drive further evolutionary changes in those populations.

Second, when organisms inherit naturally selected genes, they are, in effect, inheriting information molecularly encoded in the nucleotide sequences of DNA. Genetic information is, of course, noncognitive (see chapter 4). Nevertheless, it is information that is used to inform the expression of phenotypes in ontogenetic environments, relative to their local selective environments (J. Holland 1992, 1995; Eigen 1992). In contrast, when organisms inherit legacies of modified natural selection pressures they typically do not inherit information. Instead they inherit some of the agents in their environments that select for their genes and that thereby determine which information the organisms express (J. Holland 1995).

Third, genes and biotically modified natural selection pressures are passed on from one generation to the next by completely different processes. Genetic inheritance depends on the between-generation processes of reproduction, including sexual reproduction, which means that genes can only be transmitted to new organisms once during their lives. It also means that genes can only be transmitted to organisms by parents, and in one direction only, from parents to offspring, rather than the other way round. However, an ecological inheritance, in the form of one or more biotically modified natural selection pressures, can potentially be bequeathed by any organism to any other organism, at any stage during an organism's lifetime, and therefore within as well as between generations. It is also possible for an ecological inheritance to travel backward in generational terms because offspring may sometimes modify their parents' selective environments, as well as their own and those of their descendants.

Finally, the selective environments of organisms can be modified either by their genetic relatives or by other unrelated organisms. In fact, any organism's selective environment is potentially modifiable by any other organism that happens to be a neighbor or that shares, or that has previously shared, some common physical aspect of a

mutual environment or that is capable of exerting an indirect influence by affecting the flow of energy or materials through that environment. All such neighbors are ecologically related but they need not be genetically related. Ecological and genetic ancestors are not necessarily identical.

The way in which the two general inheritance systems operate in evolution, and how they interact with each other, is summarized in figure 1.3b. On the right of figure 1.3b genes are shown being transmitted by genetically related ancestral organisms at time t , to their genetic descendants at time $t + 1$, in the usual way. On the left, however, selected habitats, modified habitats, artifacts, or in general, ancestrally modified sources of natural selection persist or are actively or effectively transmitted by these same organisms to their descendants in their local environments (E). Thus, the selective environments encountered by the descendent organisms at time $t + 1$ do not just comprise independent sources of natural selection pressures as evolutionary theory currently implies. They stem partly from such independent environmental agents, for example, climate, weather, or physical or chemical events, but they also stem in part from sources of natural selection that have previously been modified by ancestral niche construction.

1.1.4 Adaptation

This capacity of organisms to modify some of their own selection pressures, whether between generations or within generations, also has a fourth consequence. It requires us to revise the concept of adaptation in evolution and to adjust its meaning along lines anticipated by Richard Lewontin (1983). Lewontin pointed out that contemporary evolutionary theory implicitly assumes that natural selection pressures in environments are decoupled from the adaptations of the organisms for which they select. Therefore, with some exceptions (reviewed in chapter 3), for example, those that involve frequency-dependent or habitat selection, standard theory treats sources of natural selection in environments and adaptations in organisms as independent of each other or, as Lewontin puts it: “The environment

‘poses the problem’; the organisms ‘posit solutions,’ of which the best is finally ‘chosen’” (1983, p. 276). What this classical approach overlooks, and what we are stressing here, is that the selective environments of organisms are themselves partly built by the niche-constructing activities of the organisms that they are selecting for. To quote Lewontin again: “Organisms do not adapt to their environments; they construct them out of the bits and pieces of the external world” (1983, p. 280). Therefore, some selection pressures cannot be decoupled from the adaptations of organisms. Instead they must be participants in a system of feedbacks between natural selection pressures in environments and adaptations in organisms.

We have already encountered several examples of this kind of feedback in action. For instance, the cuckoo chicks, having destroyed their host’s brood, adapt to mimic the missing broods they have killed (Davies et al. 1998). Other equally simple examples are found in spiders. One discussed by Dawkins (1996) on the basis of work by Vollrath (1988, 1992) concerns how, when its prey crashes into its web, the prey neither breaks the web nor bounces off it, but sticks to it. Many web spiders evolved the ability to make the threads of their webs sticky enough to hang on to the prey. But how are the spiders to ensure that they themselves do not get stuck to their own webs yet are free to move around on them? Dawkins offers two answers. One involves the anointing of spiders’ legs with a special oil that provides the spiders with some protection against the stickiness of their own webs, while the other involves spiders making some of the spokes of their own webs nonsticky, to allow themselves free movement along these spokes. Such examples nicely illustrate Lewontin’s point.

Lewontin (1983, 2000) argued that the classical picture of evolution can be represented formally as a pair of differential equations in time:

$$\frac{dO}{dt} = f(O, E), \quad (1.1)$$

$$\frac{dE}{dt} = g(E). \quad (1.2)$$

Equation 1.1 states that evolution, or change in the organism over time, depends on both the current state of the organism and its environment, while equation 1.2 states that environmental change depends only on environmental variables. The crucial point is that these two equations are separable. Adapted organisms are not supposed to cause any of the environmental changes that subsequently select for adapted organisms. Hence, the evolution of organisms is generally assumed to be directed exclusively by independent natural selection pressures in environments, and not at all by the niche-constructing activities of organisms. Lewontin argued that what is actually happening in nature is better represented by a pair of *coupled* differential equations

$$\frac{dO}{dt} = f(O, E), \quad (1.3)$$

$$\frac{dE}{dt} = g(O, E), \quad (1.4)$$

in which the histories of both environment and organism are functions of both environment and organism. Equations 1.3 and 1.4 describe a situation in which niche-constructing organisms and their environments are, in effect, coevolving, because they are codetermining and codirecting changes in each other. Equations 1.3 and 1.4 describe the coevolution of organism and environment in which both are acting as both causes and effects.

Evolutionary biology has provided a compelling explanation for why organisms appear so extraordinarily well suited to the environments in which they live: namely, through the action of natural selection, species have come to exhibit those characteristics that enable survival and reproduction. However, there are in fact two logically distinct routes to the evolving match between organisms and their environments: either the organism changes to suit the environment, or the environment is changed to suit the organism. The first alternative is brought about through the process of natural selection, and the second is one possible outcome of the process of niche construction. Of course, in reality these two processes can seldom be separated.

Yet the standard view is that niche construction should not be

regarded as a process in evolution because it is determined by prior natural selection. The unstated assumption is that the environmental source of the prior natural selection is independent of the organism (as formalized by eq. 1.2). However, in reality, the argument that niche construction can be disregarded because it is partly a product of natural selection makes no more sense than would the counter proposal that natural selection can be disregarded because it is partly a product of niche construction. One cannot assume that the ultimate cause of niche construction is the environments that selected for niche-constructing traits, if prior niche construction had partly caused the state of the selective environments (as formalized by eq. 1.4). Ultimately, such recursions would regress back to the beginning of life, and as niche construction is one of the defining features of life (see chapters 2 and 4), there is no stage at which we could say natural selection preceded niche construction or that selective environments preceded niche-constructing organisms. From the beginning of life, all organisms have, in part, modified their selective environments, and their ability to do so was, in part, a consequence of their naturally selected genes.

1.2 THE IMPLICATIONS

We can now start to consider some of the implications of adding niche construction to contemporary evolutionary theory. In doing so we introduce the three principal fields we shall be dealing with in later chapters: evolutionary theory itself, the relationship between evolutionary theory and ecosystem-level ecology, and the evolutionary basis of human cultural processes.

1.2.1 Implications for Evolutionary Theory

What difference does it make if the selection pressures acting on organisms stem from an independent environment or a niche-constructed environment? The principal difference is equivalent to the difference between Lewontin's coupled and uncoupled equations and can be encapsulated by one word, namely, "feedback." If organisms

evolve in response to selection pressures modified by themselves and their ancestors, there is feedback in the system. In chapters 3 and 6 of this book we will describe and analyze theoretical models that illustrate some of the differences that this feedback makes to the evolutionary process. We show how traits whose fitness depends on alterable sources of selection (recipient traits) coevolve with traits that alter sources of selection (niche-constructing traits), resulting in very different evolutionary dynamics for both traits from what would occur if each had evolved in isolation. Our models demonstrate how feedback from a population's niche construction can cause either evolutionary inertia or momentum, lead to fixation of otherwise deleterious alleles, support stable polymorphisms where none are expected, eliminate what would otherwise be stable polymorphisms, and influence levels of linkage disequilibrium. There is no escaping the conclusion that niche construction is evolutionarily consequential.

A second difference is ecological inheritance. The niche-construction perspective stresses two legacies that organisms inherit from their ancestors, genes and a modified environment with its associated selection pressures. As we document in chapter 2, ecological inheritance is likely to be ubiquitous, particularly when the widespread evidence for maternal inheritance is taken into account (Mousseau and Dingle 1991; Roach and Wulf 1987; Bernado 1996; Mousseau and Fox 1998a). Consider, for instance, the observation that most species of insects are oviparous, with the female depositing eggs on or near the food required by the offspring upon hatching (Gullan and Cranston 1994). These offspring inherit from their mother the legacy of a readily available, nutritious larval food and a nursery environment. When one considers that careful selection of appropriate sites by ovipositing females is found in the vast majority of insects and that estimates of the number of insect species range from 5 to 80 million, the pervasiveness of ecological inheritance becomes clear.

The analyses that we will present in chapters 3 and 6 demonstrate that, because of the multigenerational properties of ecological inheritance, niche construction can generate unusual evolutionary dynamics. 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 the response to selection of the recipient trait), momentum effects (popu-

lations 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; Robertson 1991; Laland et al. 1996; Mousseau and Fox 1998a,b; Wolf et al. 2000). Wherever there is ecological inheritance, a product of niche construction, the evolutionary process may include some or all of these complications.

A third implication of niche construction is that it allows acquired characteristics to play a role in the evolutionary process, in a non-Lamarckian fashion, by their influence on selective environments through niche construction. When phenotypes construct niches, they become more than simply “vehicles” for their genes (Dawkins 1989), as they may now also be responsible for modifying some of the sources of natural selection in their environments that subsequently feed back to select their own genes. However, relative to this second role of phenotypes in evolution, there is no requirement for the niche-constructing activities of phenotypes to result directly from naturally selected genes before they can influence the selection of genes in populations. Animal niche construction may depend on learning and other experiential factors, and in humans it may depend on cultural processes.

The Galápagos woodpecker finch provides a specific example (Alcock 1972). 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). While 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 that reliably contain 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 (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 behav-

ior 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. Since tool manipulation can depend in part on learning, there is a further twist to this example. Niche-constructing skills influenced by learning could modify natural selection in favor of an enhanced learning ability, and it would certainly be interesting to know whether the learning capabilities and their neural substrates in this species differ from those in closely related non-tool-using species. While the information acquired by individuals through ontogenetic processes cannot be inherited because it is erased when they die, processes such as learning can nonetheless still be of considerable importance to subsequent generations because learned knowledge can guide niche construction.

Beyond individual learning, a few species, including most vertebrates, have also evolved a capacity to learn from other individuals, and to transmit some of their own learned knowledge to others. The resulting “protocultural” processes may also underlie niche construction. An example is the spread of milk-bottle-top opening in a variety of British birds (Fisher and Hinde 1949; Hinde and Fisher 1951). These birds learned to peck open the foil cap on milk bottles and to drink the cream, and this behavior spread throughout Britain and into several other countries in Europe. Hinde and Fisher found that this behavior probably spread by local enhancement, where the birds’ attention was drawn to the milk bottles by a feeding conspecific, and after this initial tip-off, they subsequently learned on their own how to open the tops. However, further analysis by Sherry and Galef (1984) revealed that, in addition to social learning by local enhancement, milk-bottle-top opening could be acquired by other means, for example, it could also spread if the birds were merely exposed to opened milk bottles, even if there were no other birds present and performing the opening behavior. In this example, the birds’ niche-constructing behavior is propagated by local enhancement. However, by creating opened milk bottles, this niche construction biases the probability that other birds will learn to open bottles. Moreover, any selection acting on genetic variation at loci affected by milk-bottle opening would be modified in essentially the same manner as if genes were directly responsible for the behavior. For example, the

niche construction might influence selection acting on the birds' learning capacities, foraging behavior, or digestive enzymes.

Acquired niche-constructing traits have almost certainly played a significant role in the evolution of hominids among whom cultural transmission processes are ubiquitous. In chapter 6 we will describe theoretical models that reveal circumstances under which cultural transmission can overwhelm natural selection, accelerate the rate at which a favored gene spreads, initiate novel evolutionary events, and trigger hominid speciation.

1.2.2 Implications for Ecology

The niche-construction outlook may also shed light on problems traditionally considered within the domain of ecology. This is largely because of ecosystem engineering, which modulates and partly controls the flow of energy, matter, and *information* through ecosystems. Genes that interact via niche construction's effects on an external environment do not always have to be in the same population. In later chapters we will demonstrate how genes in different populations may interact with each other via biotic and even abiotic components in the environment to form environmentally mediated genotypic associations (EMGAs). Such associations may, of course, be present within a population as well (Wolf et al. 1998).

If, in a single population, genetic variation is expressed in a niche-constructing phenotype that affects natural selection acting on other genes in the same population, then the population will merely codirect its own evolution through niche construction. However, if the niche construction modifies natural selection acting on genes in a second population, then the first population will now codirect the evolution. Conceivably, the induced change in the second population could feed back to the first population in the form of another modified natural selection pressure. The two populations would therefore coevolve through niche construction.

This coevolution could also be indirect. For instance, the first population's niche construction could influence the evolution of the second population by changing an intermediate component of their

shared environment. An example here could be two species that are competing for the same environmental resource or nutrient and that coevolve because of this competition (DeAngelis 1992).

It may be possible to model many cases of coevolution by standard coevolutionary models, in terms of standard evolutionary ecology or genetics, without making any reference to either niche construction or ecological inheritance (Futuyma and Slatkin 1983; Thompson 1994; Heesterbeek and Roberts 1995; Abrams 1996). This is either because niche construction is already implicit in some of these standard models or because in a lot of cases the explicit inclusion of niche construction would make no difference.

In some cases, however, for instance, where there is interspecific exploitative competition or where prey species share a common predator, niche construction cannot be omitted from formal analyses without distorting the processes involved, and in order to describe coevolution accurately it is necessary to treat niche construction as a process in its own right (Tilman 1982; Holt 1985; Abrams 1988; DeAngelis 1992; Holt et al. 1994). When the coevolution of populations is indirect and depends on the modification of an intervening environmental component by the niche-constructing phenotypes of either one or more coevolving populations, then the explicit inclusion of niche construction and ecological inheritance adds significantly to the models. This is especially likely to be true when the intermediate environmental component concerned is abiotic. For example, if niche construction resulting from a gene in a plant population causes the soil chemistry to change in such a way that the selection on genes in a second population of plants, or possibly of microorganisms, is also changed, then the first population's niche construction will drive the evolution of the second population simply by changing the physical state of the intervening abiotic environmental variable, in this case the soil. This kind of indirect coevolution via intermediate abiota is not well described by conventional population-genetic coevolutionary models for the simple reason that abiotic components are not alive, they do not carry genes, and they cannot evolve. While the demographics of such interspecific interactions, and some issues, such as the conditions for coexistence, are well captured by ecological models, the evolutionary ramifications are comparatively underexplored. Yet abiota are continuously subject to change by niche-con-

structuring organisms (Jones et al. 1997), and any changes brought about through the activities of one population of organisms may easily serve as a legacy of modified natural selection for another. Thus adding niche construction and ecological inheritance to population-genetic coevolutionary models may make it possible to capture these interspecific interactions. As the dynamics of physical change in abiota are likely to be quite different from the dynamics of evolutionary change in populations, this kind of indirect feedback among coevolving species via intermediate abiota may generate some interesting and as yet underexplored behavior in coevolutionary systems.

Ecosystem engineering (Jones et al. 1994, 1997) further illustrates the utility of the niche-construction perspective. Jones et al. point to several ecosystem phenomena that cannot be understood in terms of energy and matter flows only. They stress the critical role played by the creation of physical structures and other modifications of their environments by organisms that partly control the distribution of resources for other species. Ecosystem engineering does not always conform to the principles of mass flow and the conservation of energy, nor to stoichiometry requirements, because ecosystem engineers are not necessarily part of these flows or cycles, but they can control them (Jones et al. 1997). We elaborate on this point in chapter 5. Gurney and Lawton (1996) have demonstrated theoretically how the efficacy with which niche construction acts to degrade a virgin habitat determines not only whether there will be no engineers, a stable population of engineers, or population cycles in the frequency of engineering, but also the extent of virgin and degraded habitat.

Evolutionary phenomena associated with niche construction complement and add to Jones et al.'s observations of the ecological repercussions of engineering. For example, when they engineer, niche-constructing organisms frequently influence their own evolution by modifying their own selective environments, perhaps by changing abiotic components or chains of such components. Second, niche-constructing organisms also influence the evolution of other populations, again often indirectly via intermediate abiotic components. Third, some organisms create new niches for themselves, for example, through technological innovation or relocation to a novel environment, which again can influence the dynamics of their ecosystems. Fourth, evolutionary and coevolutionary events can operate on

ecological time scales, which means that the dynamics of abiotic components may reflect gene frequency changes in evolving engineering species. However, these complications do not necessarily mean that ecological analyses become intractable, and in chapter 8 we describe empirical methods and theory that can be used to investigate the ecological ramifications of niche construction.

A niche-construction perspective might also promote a much closer integration between ecosystem-level ecology and evolutionary theory. Hitherto, it has proved difficult to apply evolutionary theory to ecosystems, or even to much reduced ecosystem modules, because of the presence of nonevolving abiota in ecosystems. However, the proposed extension of evolutionary theory, illustrated in figure 1.3b, is indifferent to whether any source of natural selection that is modified by niche construction is biotic or abiotic. In chapters 5 and 8 we will show how extending evolutionary theory along these lines allows abiotic ecosystem variables to be included in both evolutionary and coevolution models.

With the omission of niche construction, standard evolutionary theory underplays the full set of interactions that occur between biotic and abiotic components in ecosystems and ignores diverse forms of feedback that contribute to coevolutionary scenarios and ecosystem dynamics. This is one reason why it has hitherto been difficult to integrate process-functional and population-community ecology with each other and with standard evolutionary theory (O'Neill et al. 1986). When niche construction is incorporated, information (in the sense spelled out in chapter 4) can be seen to flow through ecosystems, and evolutionary control webs begin to emerge.

1.2.3 Implications for the Social Sciences

We shall also address the relationship between human cultural processes and human genetic evolution. At present, contemporary evolutionary theory provides a restricted basis for understanding how human cultural processes relate to human genetic processes in evolution (Laland et al. 1999). Most theory includes only one evolutionary inheritance system, genetic inheritance. It can therefore assign only one role to phenotypes in evolution, that of contributing to genetic inheri-

tance through their differential survival and reproduction. The theory does concede that human cultural activities may influence or may actually be human adaptations, or be the result of other human adaptations, and that cultural processes may also influence human fitness, but it does not concede anything more. In effect, the assumed exclusiveness of the genetic inheritance system, as espoused by classical sociobiology (Wilson 1975), renders all the other consequences of human cultural activities evolutionarily irrelevant.

Niche construction extends contemporary evolutionary theory by the introduction of two liberating innovations. First, as we have already seen, niche construction assigns a second role to phenotypes in evolution, while ecological inheritance provides a second inheritance system to which phenotypes can potentially contribute. In chapter 6 we will see that ecological inheritance is likely to have been of paramount importance in human evolution, where material culture has played a number of roles. Second, there is no requirement for niche construction to result directly from genetic variation before it can influence the selection of genetic variation. For example, niche construction may depend on learning, as in the case of the woodpecker finch and British birds discussed above, and in humans niche construction may also depend on cultural processes. To cite one well-known example, when our ancestors first domesticated cattle by agricultural niche construction, they apparently modified a natural selection pressure on a gene that enables the enzyme lactase, needed for the digestion of milk, to be synthesized by human adults (Feldman and Cavalli-Sforza 1989; Durham 1991; Holden and Mace 1997). This demonstrates how cultural processes are not just a product of human genetic evolution, but also a cause of human genetic evolution. Adding niche construction and ecological inheritance to contemporary evolutionary theory may therefore improve our understanding of the relationship between human genetic and cultural processes.

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 offer too little. Human scientists are predominantly interested in human behavior and cultural processes, rather than just genes, and as a consequence they see little useful point of contact with evolutionary theory. Our niche-construction framework may provide such a bridge because it emphasizes the active role that

organisms play in the evolutionary process. Humans are not just passive vehicles for genes, they actively modify sources of natural selection in environments. They are the ultimate niche constructors. A second reason why human scientists have difficulty with evolution is the simplicity of adaptationist accounts. Adding niche construction inevitably makes evolutionary theory more complicated, and any extra complexity must prove worthwhile to those scholars for whom environmental effects and interactions between organisms and environments are the focus of study. The relevance of the niche-construction perspective to these issues is discussed in chapter 9, where we illustrate how our framework can apply in the human sciences, providing methods and making empirically testable predictions. Indeed, many social scientists have already started to use niche construction as a useful theoretical tool.

1.3 PREVIOUS APPROACHES

If niche construction has as many consequences and implications as those we have now listed, why has it not already been incorporated into contemporary evolutionary theory? There are some theoretical devices by which contemporary evolutionary theory deals with niche construction and we discuss these in chapter 3. Here it is more appropriate to introduce some of the early forerunners of the idea, both to indicate how long the concept of niche construction has been appearing in the margins of evolutionary theory and to show that, in spite of its frequent appearances, the concept itself has received surprisingly little attention from biologists.

Perhaps the first person to draw attention to the idea of niche construction in a clear way was not even a biologist, but a physicist, Schrödinger (1944, p. 108), who did so in a lecture “Mind and Matter” given at Cambridge in 1956, as a companion to his earlier and more famous “What is Life?” lecture. It may have been because he was not a biologist that Schrödinger was able to take the outsider’s advantage of being able to discriminate between the forest and the trees more easily than those who are already in the forest.

The evolutionary biologist Ernst Mayr also made an early contribution with a much-cited quotation from his book *Animal Species and Evolution*:

A shift into a new niche or adaptive zone, is almost without exception, initiated by a change in behavior. The other adaptations to the new niche, particularly the structural ones, are acquired secondarily. With habitat and food selection—behavioral phenomena—playing a major role in the shift into new adaptive zones, the importance of behavior in initiating new evolutionary events is self-evident (Mayr 1963, p. 604).

In this passage Mayr is clearly drawing attention not just to the importance of behavior in evolution but also to how organisms can, in part, actively determine their own selective environments by niche-constructing-type activities, which *then* select for different structural adaptations. However, as Plotkin (1988) pointed out, having made this emphatic claim, Mayr himself did not follow it up. The idea was left, floating and unexploited.

Conrad Waddington (1959, 1969), another biologist, thought about niche construction in the same decade, but primarily in the context of organismal development, rather than for evolving populations. Waddington was also an early advocate of bringing developmental biology and evolutionary biology closer together, and it may have been this concern that drew his attention to the many ways in which organisms modify their own selective environments throughout their lives, by choosing and changing their own environmental niches. He called this phenotype-dependent component of both development and evolution “the exploitive system,” and he pointed out that, as far as evolutionary theory was concerned, the exploitive system had originally been left out of the modern synthesis (Huxley 1942) and that it was still being left out by contemporary evolutionary theory. Once again, possibly because Waddington was a developmental rather than an evolutionary biologist, his concept of the exploitive system was not taken up.

The next important figure in this story was the Harvard population geneticist Richard Lewontin. In the 1970s and 1980s Lewontin wrote a series of articles on adaptation. For example, Gould’s and Lewontin’s (1979) influential article “The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme” made many biologists think again about adaptation. However, that part of Lewontin’s attack on adaptationism that was based on niche construction proved much less influential, and it has drawn little re-

sponse (Futuyma 1998). Even for those biologists who accepted that Lewontin was correct, it was not immediately clear what to do about it.

Writing at roughly the same time as Lewontin, although from a very different point of view, Richard Dawkins came up with a pragmatic partial solution to this puzzle. In his book *The Extended Phenotype*, Dawkins (1982) proposed that genes not only express phenotypes, but that some of them also express “extended phenotypes” that, through the activities of organisms, reach beyond the bodies of the organisms themselves to change various components of their selective environments. To cite just one of his examples, Dawkins argued that the lodges, lakes, and dams that are built by beavers are extended phenotypes of beaver genes.

As far as this argument goes it is obviously right, but it is also too restricted. For instance, Dawkins recognized that any genes that are expressed in an extended phenotype should affect the probability of the survival and reproduction of the organism that is carrying them, and therefore their own representation in the next generation. However, Dawkins did not consider that the same gene might also affect the fitness of other genotypes, at other genetic loci, by changing their selective environment. A beaver’s dam modifies many selection pressures in the beaver environment, some of which are likely to feed back to affect the fitness of genes that are expressed in quite different traits, such as their teeth, tails, feeding behavior, susceptibility to predation, diseases, life-history strategies, and social systems. Similar limitations constrain almost all the other approaches to niche construction in contemporary evolutionary theory, which are discussed in more detail in chapter 3.

Aside from the advocates of niche construction that we have mentioned, a number of other researchers have pursued and in some cases continue to pursue related ideas (Levins and Lewontin 1985; Wilson 1985; West-Eberhart 1987; West et al. 1988; Bateson 1988; Plotkin 1988; Weislo 1989; Holt and Gaines 1992; Michel and Moore 1995; Brandon and Antonovics 1996; Moore et al. 1997; Wolf et al. 1998; Oyama et al. 2001; Sterelny 2001; Jablonka 2001; Griffiths and Gray 2001). There were, and still are, other scientists who have resisted the idea, for a variety of different reasons. For the moment, we will introduce only the two principal reasons. The first and probably the

most straightforward reason for rejecting niche construction is a belief that it does not exist. For example, both George Gaylord Simpson (1949) and Theodore Dobzhansky (1955) maintained that, humans aside, organisms either do not construct or regulate their niches to any significant degree, or their impact on their environments is invariably too weak, too transient, or too capricious to have any substantial effect on selection pressures. They argued that there are always other more potent independent agents in environments that invariably override the effects of the organisms themselves, thereby preventing organisms from influencing either their own natural selection or the natural selection of their successors. Ultimately, this is an empirical issue, but there is already sufficient evidence to show that organisms can, and indeed do, modify at least some of their own natural selection pressures with sufficient consistency to render this older critical position implausible (see chapter 2).

Originally, this kind of criticism may have stemmed from an intuition that the environment is so vast, and organisms are so small, that the capacity of organisms to change their environments must be negligible. This intuition overlooks two points. One is that natural selection is local—indeed, it is famous for being “myopic.” Niche construction becomes an effective codirecting agent in evolution through the modification of local selection pressures. The second point is that, in spite of its local ramifications, because niche construction may be influenced by inherited genes and the same genes may be inherited for many generations, niche construction may sometimes generate some truly large-scale changes in the wider world through the accumulation of effects over long spans of time. The production of oxygen by photosynthetic organisms is a clear example.

Resistance to the idea of niche construction usually takes a different form today. From many personal communications, we have found that most contemporary biologists are prepared to admit that niche construction occurs, and that when it occurs it is bound to have some ecological consequences, but they may still doubt whether it has anything other than trivial evolutionary consequences. Advocates of this position typically maintain that it does not matter much whether natural selection pressures originate from niche-constructing organisms or from other independent sources in environments, as the process of evolution will still be the same. Others accept that sometimes niche

construction does affect the process but argue that the effect is not great enough to require anything more than some ad hoc adjustments to contemporary evolutionary theory. Such protagonists would suggest that niche construction is not sufficiently consequential to justify the kind of major revision of evolutionary theory that we are proposing here (fig. 1.3b). In the subsequent chapters we expand on the consequences of niche consequences that have been badly underestimated in the past and are still being underestimated today.

1.4 A PRECIS OF SUBSEQUENT CHAPTERS

The remaining chapters in this book represent a summary of our attempt to begin to redress the neglect of niche construction as an evolutionary agent. In chapter 2 we begin with definitions of niche construction, ecological inheritance, and other important terminology. Chapter 2 also presents a systematic collation and categorization of examples of niche construction, as well as of traits that appear to have evolved as a consequence of selection pressures modified by niche construction. These empirical data illustrate the ubiquity of niche construction.

Chapter 3 discusses previous attempts to handle aspects of niche construction, including frequency- and density-dependent selection, habitat selection, coevolution, indirect genetic effects, maternal inheritance, and various other approaches. We show that, while each of these separate bodies of theory has features germane to niche construction, none of them captures all of the pertinent characteristics. Thus, aside from our own analyses, there has been no attempt to explore the evolutionary consequences of niche construction in a systematic and general manner. Nonetheless, findings from these disparate approaches strongly suggest that niche construction is likely to be an important evolutionary process.

Chapter 3 goes on to investigate the likely evolutionary consequences of niche construction by presenting theoretical population-genetic models that explicitly incorporate the process of niche construction into the evolutionary dynamic. If niche construction is as important an evolutionary process as we claim, then its inclusion

should make a significant difference to the behavior of theoretical models and should generate some unusual and hitherto unpredicted dynamics. In the text of chapter 3 we describe the findings of our formal analyses, with all technical and mathematical details relegated to the appendixes. The results of these analyses clearly demonstrate that there are myriad ways by which niche construction is likely to have an evolutionary impact.

There is one prerequisite of evolutionary theory that is often taken for granted. Natural selection can obviously only work when it is fed with a continuous supply of organismal diversity. Superficially, however, organisms appear to violate the second law of thermodynamics merely by staying alive and reproducing, since this law dictates that net entropy always increases and that complex, concentrated stores of energy will inevitably break down. In chapter 4 we ask what characteristics any organism must have *merely to live*. Drawing from theoretical developments in physics and thermodynamics, which offer a description of the Maxwell's-demon-type properties any agent needs to drive a system out of equilibrium, we identify the universal properties that niche construction must have if organisms are not to violate physical laws. As some characteristics of niche construction are universal, it follows that some aspects of the impact that niche-constructing organisms have on their environments will also be universal. Moreover, we suggest that, like natural selection, niche construction is a selective process and that, distinct from other evolutionary processes (e.g., drift, mutation), it introduces directedness to the evolutionary process.

If there are universal and characteristic features of niche construction then it follows that the evolutionary process must have universal and characteristic impacts on the local environments of evolving species. This raises the possibility that niche construction may have implications for ecosystem-level ecology and that a niche-construction perspective may shed light on problems traditionally considered within the domain of ecology. We spell out these implications in chapter 5, where we draw heavily on the insights of ecosystem-engineering researchers. We also illustrate how, with niche construction, evolutionary theory can help describe ecosystem dynamics in spite of the fact that ecosystems include abiotic components. An extended

evolutionary theory that takes account of how evolving organisms affect both biota and abiota can provide an integrative evolutionary framework for ecology.

In chapter 6 we address the repercussions of the niche-construction perspective for the human social sciences. A focus on niche construction has important implications for the relationship between genetic evolution and cultural processes. By integrating developments in niche construction and gene-culture coevolutionary theory and explicitly recognizing the guiding role of learning and cultural processes in the niche construction of complex organisms, we develop a new evolutionary framework for the human sciences. This conceptual model is designed to act as a hypothesis-generating framework around which human scientists can structure evolutionary approaches to their disciplines.

In the final section of chapter 6 we illustrate how aspects of this new evolutionary framework can be translated into formal models that illustrate how cultural niche construction may have driven genetic evolution throughout the last two million years. Many results characteristic of gene-based niche construction are also found for cultural niche construction, although cultural niche construction may well have been, and may continue to be, even more potent. Any bias in cultural transmission, or differences in the rate at which alternative behavior patterns are acquired, can increase the impact of niche construction over and above that resulting from genes. Where cultural transmission and natural selection conflict, there is a broad range of circumstances under which cultural transmission can overwhelm natural selection. This is one reason why maladaptive behavior is possible among humans (Cavalli-Sforza and Feldman 1981).

We maintain that these proposed extensions fundamentally alter evolutionary theory. If we are correct, then there should be a set of empirical predictions that would generate data consistent with the niche-construction perspective and inconsistent with more conventional evolutionary perspectives. We acknowledge that unless and until we, or others, generate data that are irreconcilable with conventional neo-Darwinism, or at least are more consistent with the niche-construction perspective, the revisions to evolutionary thinking that we suggest are unlikely to become accepted by the biological community. Consequently, in chapters 7–9 we describe how our hypoth-

eses concerning the evolutionary role of niche construction may be tested and suggest methods for doing so.

Empirical methods and predictions for evolutionary biology, ecology, and the social sciences, respectively, are spelled out in chapters 7, 8, and 9. These methods range from experiments that investigate the consequences of canceling or enhancing a population's capacity for niche construction, to comparative analyses that explore the phylogeny of trait evolution across related species, to directly testing the predictions of our theoretical models. In these chapters we also suggest areas in which our perspective may stimulate empirical study. There is a rich array of possibilities for testing the evolutionary credentials of niche construction, and we hope that this new perspective will stimulate empirical research in the biological and social sciences.

Finally, chapter 10 integrates these findings to make the case that niche construction should be regarded as a significant evolutionary process in its own right; part of an "extended evolutionary theory." For readers without the time or inclination to read all the preceding chapters, this final statement summarizes the contents of the book and our overall argument. It describes why we believe not only that the niche-construction perspective is a more accurate depiction of the evolutionary process than the conventional view, but that it will eventually prove to be a more useful evolutionary framework. We suggest that niche construction is not just an important addition to current evolutionary theory; it requires a reformulation of evolutionary theory. When evolutionary biologists and researchers in related disciplines start using niche construction as a means of formulating hypotheses and generating insights in their fields, then niche construction will be seen to earn its keep.