

NOTES AND COMMENTS

NICHE CONSTRUCTION

Organisms, through their metabolism, their activities, and their choices, define, partly create, and partly destroy their own niches. We refer to these phenomena as “niche construction.” Here we argue that niche construction regularly modifies both biotic and abiotic sources of natural selection in environments and, in so doing, generates a form of feedback in evolution that is not yet fully appreciated by contemporary evolutionary theory (Lewontin 1978, 1983; Odling-Smee 1988, in press).

Adaptation is generally thought of as a process by which natural selection shapes organisms to fit preestablished environmental “templates.” Environments pose “problems,” and those organisms best equipped to deal with the problems leave the most offspring. Despite the recognition that forces independent of organisms often change the worlds to which populations adapt (Van Valen 1973), the changes that organisms bring about in their own worlds are rarely considered in evolutionary analyses. Yet, to varying degrees, organisms choose their own habitats, mates, and resources and construct important components of their local environments such as nests, holes, burrows, paths, webs, dams, and chemical environments. Many organisms also choose, protect, and provision “nursery” environments for their offspring. Organisms not only adapt to environments, but in part also construct them (Lewontin 1983). Hence, many of the sources of natural selection to which organisms are exposed exist partly as a consequence of the niche-constructing activities of past and present generations of organisms.

There are numerous cases of organisms modifying their own selective environments in nontrivial ways, by changing their surroundings or by constructing artifacts (Von Frisch 1975; Hansell 1984). One early example was described by Darwin (1881). Earthworms, through their burrowing activities, their dragging organic material into the soil, their mixing it with inorganic material, and their casting, which serves as a basis for microbial activity, change both the structure and chemistry of soils (Lee 1985). As a result of the accumulated effects of past generations of earthworm niche construction, present generations inhabit radically altered environments and are exposed to changing sets of selection pressures.

There is also considerable evidence of evolutionary responses to self-induced selection pressures. For instance, social bees, wasps, ants, and termites construct

elaborate nests that then mediate selection for many nest regulatory, maintenance, and defense behaviors (Rothenbuhler 1964; Spradbery 1973; Von Frisch 1975; Mathews and Mathews 1978; Hansell 1984). Many species of fish, amphibians, reptiles, birds, and mammals construct nests and burrows, which then influence further selection. For example, comparative evidence suggests that the complex burrow systems excavated by moles, rats, badgers, and marmots, with their underground passages, interconnected chambers, and multiple entrances, have served as the source of selection for defense, maintenance, and regulation behaviors and components of mating rituals (Von Frisch 1975; Hansell 1984).

Plants, too, change the chemical nature, pattern of nutrient cycling, temperature, humidity, and fertility of the soils in which they live (Ricklefs 1990). They may even affect local climates, the amount of precipitation, and the water cycle (Shukla et al. 1990). Many plants also change both their own and other species' local environments via allelopathy (Rice 1984), while pine and chaparral tree species facilitate forest fires by accumulating oils or litter (Mount 1964; Allen and Starr 1982). These species have evolved a resistance to fire and, in some pine species that require a fire before their seeds will germinate, a dependency on it (Allen and Starr 1982).

THE EVOLUTIONARY CONSEQUENCES OF NICHE CONSTRUCTION

These examples, and others (Lewontin 1982, 1983), suggest that niche construction may be a general phenomenon, that it is not restricted to a few isolated species or taxa, and that feedback from phenotypically modified sources of selection in environments has evolutionary as well as ecological consequences. Although several topics in contemporary population biology are already concerned with the evolutionary consequences of the changes that organisms bring about in their own environments (e.g., habitat, frequency- and density-dependent selection), so far these analyses have only focused on genetic loci that influence the production of the niche-constructing phenotype itself. What is missing is any exploration of the feedback effects on other genetic loci. A more general body of theory is required.

In order to encourage the development of this theory, in what follows we discuss some evolutionary consequences of niche construction and detail why it is likely to be of significance to the biological sciences.

EXTRAGENETIC INHERITANCE

Currently, evolutionary theory rests heavily on the assumption that only genes are transmitted from generation to generation, the principal exception being cultural inheritance (Feldman and Cavalli-Sforza 1976; Boyd and Richerson 1985). However, ancestral niche-constructing organisms effectively transmit legacies of modified natural selection pressures in their environments to their descendants. This extragenetic inheritance has previously been called an "exploitive system" (Waddington 1959), an "ontogenetic inheritance" (West et al. 1988), and an "ecological inheritance" (Odling-Smee 1988). We will introduce it in stages.

If, in each generation, each organism only modifies its environment temporarily or inconsistently, then there will be no cumulative or consistent modification of any source of natural selection in its population's environment. If, however, in each generation, each organism repeatedly changes its own ontogenetic environment in the same way, because each individual inherits the same genes causing it to do so, then ancestral organisms can modify a source of natural selection for their descendants by repetitive niche construction. The environmental consequences of such niche construction may be transitory and may still be restricted to single generations only, but the same induced environmental change is reimposed sufficiently often, for sufficient generations, to serve as a significant source of selection.

For example, individual web spiders repeatedly make webs in their environments, generation after generation, because they repeatedly inherit genes instructing them to do so. Subsequently, the consistent presence of a web in each spider's environment may, over many generations, feed back to become the source of a new selection pressure for a further phenotypic change in the spiders, such as the building by *Cyclosa* of dummy spiders in their webs to divert the attention of avian predators (Edmunds 1974). Yet, this kind of feedback does not introduce an extragenetic inheritance in evolution, because no consequence of niche construction is transmitted through an external environment from one generation to the next.

In more complex cases, inherited genes instruct organisms to modify repeatedly the ontogenetic environments of their offspring as well as, or instead of, their own. Here the consequences of niche construction are effectively "transmitted" from one generation to the next via an external environment, in the form of a parentally modified source of natural selection for their offspring. This transmittal is sufficient to establish an extragenetic inheritance system in evolution. Offspring now receive a dual inheritance from their parents, genes relative to their selective environments, and at least some parentally modified sources of selection in their environments relative to their genes.

The cuckoo is an example. Cuckoo parents repeatedly select host nests for their offspring, generation after generation, thereby bequeathing modified selection pressures as well as genes to their offspring. These modified selection pressures have then apparently selected for changed adaptations in the offspring, such as a short incubation period or the behavioral ejection by newly hatched cuckoo chicks of host eggs from the parasitized nests. Also, cuckoos that are raised in the nests of a particular host species may preferentially parasitize that host species in whose nests they were originally raised themselves when they mature, possibly learning the host characteristics through imprinting (Krebs and Davies 1993). This kind of extragenetic inheritance is currently modeled as a non-Mendelian maternal inheritance (Cowly and Atchley 1992; Schluter and Gustafsson 1993). Maternal inheritance can generate some counterintuitive results, including temporarily reversed evolutionary responses to selection, and time lags that may result in populations continuing to evolve after selection has ceased by an "evolutionary momentum" (Feldman and Cavalli-Sforza 1976; Kirkpatrick and Lande 1989).

Maternal inheritance is, however, a special case, and the effects of niche con-

struction generalize to multiple generations and to multiple ancestors, not just mothers. For example, suppose a niche-constructing behavior is influenced by genetic variation at one set of loci, that it spreads through a population over many generations, and that it progressively changes the frequency of some resource in the environment as it does so. Suppose further that the frequency of the resource, now a part of an extragenetic inheritance, feeds back to the population to influence selection at a second set of loci. In these circumstances, a time lag should develop between the change in frequency of alleles at the niche construction loci and the response to a frequency-dependent modified selection pressure at the recipient loci, the only difference being that here the time lag is likely to take many more generations to build up.

Darwin's earthworms are an example. Suppose a first genetic locus influences some niche-constructing behavior, such as soil processing or burrow lining, which subsequently affects the amount of topsoil or the soil nutrients in the earthworms' environment. Another locus expresses a phenotype that is affected by soil conditions, such as the structure of the epidermis or the amount of mucus secreted. In this case, ancestral niche construction by many generations of earthworms, due to the first locus, will eventually feed back to the second locus and change its selection, but only after many generations of niche construction. Here again, the effect of the time lag should be to create an evolutionary "momentum," such that if the selection pressures at the first locus are relaxed or reversed, the response at the second locus should continue in the original direction for a number of additional generations. Moreover, assuming many generations are required to modify natural selection on a population, it might not be able to evolve fast enough to prevent the genetic variation on which its eventual response relies from being prematurely lost. This possibility also means that once a population reaches a stable equilibrium, it may take a greater period of time, or stronger selection, for the population to move away from it.

INDIRECT GENE INTERACTIONS

Niche construction provides a way in which the differential phenotypic expression of genotypes at one locus can be influenced by the genotype at another locus, indirectly via the external environment. For instance, the pink coloration characteristic of flamingo species is extracted from the carotenoid pigmentation of the crustacea they digest (Fox 1979). Here the genes influencing flamingo prey choice interact with those underlying pigment extraction and utilization, via the food resources in their environment. In several respects, the genetic basis of this feedback is reminiscent of epistasis. In contrast to conventional epistasis, however, niche construction can generate interactions between genes in different populations, even different species. For example, the genes that underlie those activities of earthworms that modify soil structure, thereby enhancing plant yields (Lee 1985), have influenced the expression of genes in the plant population affecting growth. Thus, the niche-constructing outputs of individuals not only change selective environments, which feed back to alter the fitnesses of alleles at other loci, but may also influence the phenotypic expression of those alleles in ontoge-

netic environments (West et al. 1988). The effect of these interactions, which influence both the nature of the variants subjected to selection and the pattern of selection acting on those variants, is to introduce the kind of feedback loops between populations and their environments that Robertson (1991) suggests may make a considerable difference in evolution.

SYNTHESIZING EVOLUTIONARY BIOLOGY AND ECOLOGY

Because niche construction may apply to interactions between genes in the same population, or in different populations, it provides a mechanism for driving populations to coevolve in ecosystems. Populations may affect each other not only directly in the ways that are already modeled by coevolutionary theory, as, for instance, in host-parasite coevolution (Futuyma and Slatkin 1983), but also indirectly via their impact on some intermediate abiotic component in a shared ecosystem, as in competition for a chemical or water resource. 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 of a gene in a second population, of plants or microorganisms, is changed, then the first population's niche construction will drive the evolution of the second population simply by changing the physical state of this abiotic ecosystem component. Since the dynamics of the intermediate abiotic component may be qualitatively quite different from either the frequency changes in the genes that underlie the niche construction or the number of niche-constructing organisms in the first population, this indirect feedback between species may generate some interesting—and as yet unexplored—behavior in coevolutionary systems.

Accounting for the evolution and prevalence of mutualistic interactions is a stubborn problem for theoretical population biologists, who usually assume that there is some cost to the donor (Roughgarden 1975; Mesterton-Gibbons and Dugatkin 1992). Recent years, however, have seen a change in thinking about mutualism, with increasing emphasis placed on the fact that many mutualisms involve the transfer of incidental by-products, at no cost to the donor (West-Eberhard 1975; Brown 1983; Janzen 1985; Connor 1986; Mesterton-Gibbons and Dugatkin 1992). For example, seed predators often benefit the host plant through the dispersal of its seeds at no cost to themselves (Janzen 1985). These by-products, which are clearly a component of a population's niche construction, often serve as the source of selection for interspecific investment in their production (Connor 1986). For instance, fruit represents investment in seed dispersers (Thompson 1982). A thorough understanding of these coevolutionary dynamics may involve formal recognition that the niche-constructing activities of organisms can change selection pressures and thereby initiate mutualistic interactions.

A SECOND ROLE FOR PHENOTYPES IN EVOLUTION

When phenotypes niche construct, they can no longer be thought of as simply “vehicles for genes,” since they are now also responsible for modifying some of the sources of selection in their environments that may subsequently feed back

to select their genes. Moreover, there is no requirement for niche construction to result directly from genetic variation before it can influence the selection of genetic variation. For instance, niche construction can depend on learning, as is the case for the British tits that may have changed their own selection pressures by opening foil milk-bottle tops, thereby gaining access to a new resource. The evolutionary consequences of this learned innovation are unknown, but it is possible that this new resource may now be selecting for some further change in these tits—for instance, for different digestive enzymes—or for improved learning ability (Fisher and Hinde 1949; Sherry and Galef 1984). Similarly, niche construction can also depend on culture, as happens when humans increase the frequency of the sickle-cell allele in their own populations by unwittingly increasing the prevalence of malaria in their environments through their agricultural practices (Durham 1991). The consequences for a gene at the second locus are the same, provided the effect of the niche construction on the environmental resources that constitute the source of selection is unchanged. The net result is an additional role for phenotypes in evolution. Phenotypes not only survive and reproduce differentially in the face of natural selection and chance but also modify some sources of selection in their environments by niche construction.

RELATIVIZATION OF EVOLUTIONARY BIOLOGY

On the basis of empirical evidence, Lewontin (1978, 1982, 1983) has argued that the “metaphor of adaptation” should be replaced by a “metaphor of construction.” However, the acceptance of Lewontin’s position demands more than just semantic adjustments to evolutionary theory. Niche construction changes the dynamic of the evolutionary process in fundamental ways because it precludes a description of evolutionary change relative only to autonomous environments. Instead, evolution now consists of endless cycles of natural selection and niche construction. Equally, it is no longer tenable to assume that the only way organisms can contribute to evolutionary descent is by passing on fit or unfit genes to their descendants relative to their environments, because they can also pass on modifications in those environments that are better or worse suited to their genes. Adaptation becomes a two-way street.

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