Conceptual Evolution: Replication

Dawkins introduced the notions of replicator and vehicle because of their generality and because of the common associations of such terms as *gene* and *organism*. However, *replicator* and *vehicle* also have their connotations. As far as I can see, the connotations of the term *replicator* are entirely appropriate whereas those of *vehicle* are not. Vehicles are the sort of thing that agents ride around in. More than this, the agents are in control. The agents steer and the vehicles follow dumbly. The picture that Dawkins's terminology elicits is that of genes controlling helpless and hapless organisms. Although Dawkins explicitly assigns an evolutionary role to both replicators and vehicles, his terminology is likely to mislead one into treating vehicles as passive tools in the hands of all-powerful replicators. As Sober (1984, p. 255) repeatedly emphasizes, "The units of selection controversy began as a question about causation." For this reason, I prefer *interactor* to *vehicle* (see also Williams 1985).

Dawkins intends replicator to apply to any entity that happens to possess the appropriate characteristics. In biological evolution, he insists that only genes function as replicators (the paramecium example notwithstanding). However, Dawkins (1976, p. 68) recognizes that in other sorts of selection processes other entities might function as replicators—for example, in "cultural analogues of evolution." He terms the cultural analogues of genes memes (See also Semon 1904). According to Dawkins, genes and memes are equally replicators. If memes are to function as replicators, then they must have structure and be able to pass on this structure through successive replications. If conceptual change is to occur by means of selection processes, memes cannot exist in some other "world" (Popper 1972) but must exist in the material world—in brains, computers, books, etc. A second reason for preferring interactor to vehicle is that the father of evolutionary epistemology, Donald Campbell (1979), uses vehicle to refer to replication in both biological and conceptual evolution. Genes are the vehicles that transmit the information in biological evolution, whereas everything from stone tablets and papyrus to magnetic tapes and electronic chips can serve as the physical vehicles in conceptual evolution. Using vehicle to refer both to interactors and to the physical basis of replication begs for misunderstanding, and misunderstanding comes along easily enough on its own. One need not beg for it.

Thus far, the burgeoning literature on conceptual change as a selection process has concentrated primarily on conceptual replication and how it differs (or does not differ) from replication in biological evolution. The most common alleged disanalogies between the two processes are that conceptual evolution is Lamarckian whereas biological evolution is not, that conceptual evolution is not biparental the way that biological evolution

tion is, that cross-lineage borrowing is common in conceptual evolution but rare or nonexistent in biological evolution, and that conceptual evolution can be and often is insightful and intentional whereas biological evolution is blind and mechanical. Elsewhere I have argued that these alleged disanalogies are exaggerated, and that they stem from the failure to distinguish adequately between gene-based biological evolution and meme-based conceptual change (Hull 1982).

Though proponents and opponents of treating conceptual change as a selection process have often claimed that conceptual evolution is somehow "Lamarckian," no one has explained at much length what this term means in connection with conceptual change. In biological evolution, inheritance counts as "Lamarckian" if adaptive changes in the phenotype of an organism were transmitted to the genetic material and thereafter inherited by the organism's progeny. Acquired characteristics must be inherited, not just transmitted. The above example of alterations in the cortex of a paramecium is not an example of Lamarckian inheritance because the genetic material is bypassed. Social learning would be literally Lamarckian if the knowledge that an organism acquired about its environment somehow came to be encoded in its genetic material and thereafter was inherited by its progeny. As far as I know, none of the advocates of an evolutionary analysis of conceptual change view social learning in such a literal fashion. The whole point of social learning is that information is transmitted independently of genes. If social learning is Lamarckian, it must be so only in a metaphorical sense of this term. Such conceptual entities as memes must be substituted for genes, but it should be noted that memes are analogous to genes, not to characteristics. Hence, their transmission does not count as an instance of the inheritance of acquired characteristics precisely because they are not the analogues of characteristics. In sum, on a literal interpretation, social learning is not an example of the inheritances of acquired characteristics because inheritance is not involved (just transmission). On a metaphorical interpretation, social learning does not count as an instance of the inheritance of acquired characteristics because the things being passed on are analogues of genes, not of characteristics. Social learning is, if anything, an instance of the inheritance of acquired memes. One organism can certainly give another fleas, but this is hardly an instance of the inheritance of acquired characteristics. Social learning is to some extent "guided" (Boyd and Richerson 1985), but to call it on that account "Lamarckian" is to use this term in its most caricatured form, as if giraffes got such long necks by striving to reach the leaves at the tops of trees.

In this connection, commentators often state that biological evolution is always "vertical" whereas conceptual evolution is likely to be "horizontal." By this they mean that the transmission of characteristics in biological evolution is always from parent to offspring (i.e., inheritance). Characteris-

tics always follow genes. In point of fact, biological evolution is not always vertical, even when characteristics follow genes. For example, it is horizontal when bacteria, paramecia, etc. exchange genetic material. Horizontal transmission can even be cross-lineage, as when viruses pick up genes from an organism belonging to one species and transmit them to an organism belonging to a different species. In conceptual contexts, parents can instruct their offspring, but they can also teach things to their elders, to others of their own biological generation, or to younger organisms to which they are not closely related. From the perspective of gene lineages, considerable cross-lineage borrowing occurs in conceptual evolution, but all this shows is that the relevant lineages for conceptual evolution are not gene lineages. The transmission of memes is what determines conceptual lineages. Hence, by definition, if a significant amount of cross-lineage borrowing is taking place between two conceptual lineages, these are not two conceptual lineages but one. The situation is exactly analogous to the situation in biological evolution. If a significant amount of gene exchange is taking place between two putative lineages, these lineages count not as two lineages but one (Hull 1982, 1984, 1985a).

Sometimes conceptual change is "biparental"—that is, ideas are obtained from two different sources and combined—but quite obviously information can be transmitted from a single source to another or combined from several sources. If the transmission of genes were actually always biparental, this would be an important difference between biological and conceptual evolution, but of course it is not. Both asexual reproduction and polyploidy are common. In general, those who oppose treating conceptual change as evolutionary reason from an extremely impoverished view of biological evolution to the context of conceptual evolution. Their view of biological evolution is so narrow that most biological evolution does not fit.

In this same connection, commentators on an evolutionary analysis of conceptual change are nearly unanimous in noting that conceptual change can occur much more rapidly than biological evolution (for an exception see Boyd and Richerson 1985). For example, under the most extreme selection pressures, a mutation that arose in the time of Julius Caesar would only now be becoming widely distributed in the human species. In this same time interval, conceptual systems have undergone great changes several times over. But the preceding contrast depends on taking calendar time as the appropriate time frame for both biological and conceptual evolution, when it is adequate for neither. Biological evolution is phylogenetic; it occurs only through a succession of biological generations. Individual learning is ontogenetic. It takes place within the confines of a single biological generation. In this respect it is like the immune system. Social learning is both ontogenetic and phylogenetic. It can occur both

within and between biological generations. However, neither calendar time nor biological generations is the univocal time frame appropriate for either biological or conceptual selection processes.

With respect to calendar time, bacteria reproduce much more quickly than elephants; from the perspective of generations, they reproduce at the same speed. One reason why claims about molecular clocks caused such consternation among evolutionary biologists is that they were supposed to be constant with respect to calendar time, regardless of the generation time of the organisms in which these changes were occurring. With respect to the evolutionary process, a variety of time frames are relevant. For example, for mutation, cell cycle time is more appropriate than the generation time of the entire organism (Lewin 1985); however, for the evolutionary process as such, calendar time enters in only with respect to ecological interactions. For example, because of differences in generation time, new strains of bacteria and viruses pose dangers for organisms with slower generation times. They themselves cannot evolve fast enough to keep up with the bacteria and viruses, but their immune systems can. As a result of the preceding considerations, the appropriate time frame for replication in conceptual evolution is generational. Each time a meme is replicated, that is a generation. Thus, in the course of his biological lifetime, a geometry teacher may replicate the Pythagorean theorem hundreds of times. From the perspective of physical time, conceptual generations are much shorter than certain biological generations and longer than others; but from the perspective of generations per se, biological and conceptual evolution take place at the same speed—by definition.

The only frequently alleged difference between biological and conceptual evolution that does not arise from a straightforward misunderstanding concerns intentionality. Intentionality certainly plays a role in biological evolution. Both human and nonhuman organisms strive to elude predators, find mates, etc. However, a small number of the organisms belonging to the human species are aware that species evolve. As a result, they are in a position to influence that evolution consciously. Members of all species influence the evolution of their own and other species unintentionally, but the few people who acknowledge the existence of biological evolution and understand it sufficiently are in a position to direct it intentionally. We already do so in the case of domesticated plants and animals. Most of the changes that we have wrought in these creatures have been unintentional, but some have been consciously brought about. In the past, we have had to wait around until a particular variation happened to crop up. We are now in the position to introduce specific variations and to select the resulting variants. It would seem that we have always been in this position in cases of conceptual change. For instance, scientists often strive to solve problems and in doing so intentionally direct the course of conceptual

evolution. In conceptual evolution both the introduction of variations and their selection can be done consciously toward certain ends.

Whether or not intentionality presents a significant disanalogy between biological and conceptual evolution depends upon how we distinguish between the two. Two criteria have been suggested: the sort of entity that functions as the relevant replicators (genes versus memes) and the source of new variants and/or their subsequent selection (intentional or not). Given these two criteria, four combinations are possible. Two combinations pose no problems. Most biological change is gene-based and nonintentional. Neither the introduction of new variants nor their selection is in any sense intentional. Some conceptual change, (probably not much) is meme-based and intentional. A conscious agent either generated the conceptual variant intentionally, or subsequently selected this variant, or both. But the other two combinations raise some difficulties. Some change is gene-based and intentional—selective breeding. The things being changed are genes, and the traits that are being selected are being transmitted via genes. However, the agent involved is conscious of what he or she is doing and is doing it intentionally. In Darwin's day the presence of a conscious agent in artificial selection and the absence of such an agent in natural selection was considered extremely important. In reasoning from artificial selection to natural selection, Darwin took himself to be reasoning by analogy. Just as breeders could select wisely, so could nature (Young 1971; Ruse 1975; Waters 1986). However, today artificial selection is considered to be a special case of natural selection and part of the legitimate subject matter of evolutionary biology—the presence of an intentional agent notwithstanding (Rosenberg 1985, p. 171).

The final combination is unintentional meme-based change. If Freud is right, understanding, inference, conscious choice, and the like play much less of a role in human behavior than his more rationalistic contemporaries thought. Although I am hardly a fan of Freud, I have a fairly skeptical attitude toward the role of these factors in human affairs. The rule that human beings seem to follow is to engage the brain only when all else fails—and usually not even then. However, the relevant issue is not the frequency of the relevant behavior but its classification as biological or conceptual. If the presence of intentionality is the crucial difference between biological and conceptual evolution, then artificial selection belongs in the province of conceptual evolution and all the unintentional conceptual changes produced by humankind belong to neither. I am not sure what choices the critics of an evolutionary analysis of conceptual change are likely to make in these matters. However, further discussion requires the introduction of the second aspect of selection processes, interaction. (For a more extensive discussion of the place of intentionality in nature, see Searle 1984.)

Conceptual Evolution: Interaction

In biological evolution, entities at numerous levels of organization interact with their respective environments as cohesive wholes in such a way that replication is differential. Some sperm can swim faster than others, some antibodies are more effective than others, some kidneys are better able to eliminate wastes, some organisms can withstand dessication for longer periods of time, some beehives can keep their internal temperature more constant than others, and sexual reproduction may have arisen as a species-level adaptation to increase speciation rates (Lewontin 1970). Any characterization of biological evolution that leaves out reference to interactors and their adaptations is leaving out half the causal story. The same observation holds for conceptual change. If the notion of conceptual replication makes sense, the task of identifying conceptual interactors remains. To put the issue in more restricted terms: Analogues to the genome-phenome distinction must be specified in conceptual evolution. In conceptual change, memes physically embody information in their structure. This structure is differentially perpetuated. But what is responsible for certain information proliferating while other information is lost?

One sure sign in biological contexts that autocatalysis (the transmission of information in replication sequences) is being replaced by heterocatalysis (the translation of information contained in the structure of the replicators) is a precipitous loss of "potential" information. In sexual reproduction, each genotype is almost always instantiated by a single genotoken, and this single genotoken usually gets to produce only a single phenotoken. Hence, in such circumstances, each genotype is selected via a single phenotoken. In cases of cloning, particular genotypes are represented by several genotokens. Hence, they can be tested by means of several phenotokens. But even in such cases, numerous alternative representations are never realized. Biological evolution seems "unfair" on a host of counts. One of them is that neither single genes nor entire genomes ever get to show their "real stuff." They succeed or fail in replicating themselves, depending on a relatively small number of actual exemplifications of all possible exemplifications permitted by the information they contain.

The same is true of conceptual replicators. Natural languages serve many functions. One of them is communication. Another is description, and part of what is communicated are these descriptions. Communication is the analogue to replication, whereas the testing of descriptive statements is the analogue to interaction—the translation of the information contained in a descriptive statement in such a way that it can be tested. A single gene corresponds roughly to a single concept, an entire genome to a more inclusive conceptual entity such as a scientific theory. Just as single genes never confront their environments in isolation, single concepts are never tested in isolation.

Philosophers have argued at great length that the meaning of a theoretical term is never exhausted by the various operational "definitions" used to apply it. A particular experiment or observation bears on only one small part of the meaning of the theoretical claim. For descriptive statements, the analogue to the interactor-environment interface is testing. Any minimally sophisticated conceptual system implies a huge array of observational consequences. Only a very few are ever likely to be tested, but the system will be accepted, rejected, ignored, or modified on the basis of these few tests. Conceptual change is hardly less unfair than biological evolution. Sometimes just the right test is run in just the right way; at other times an unfortunate choice results in the rejection of a theory. Mendel's work on garden peas is an example of the first sort; his choice of a particular species of Hieracium to extend his theory is an instance of the second sort. Garden peas could not have been a better choice. They exemplify what has come to be known as Mendel's laws with admirable clarity. His second choice could not have been worse. Inheritance in *Hieracium* is near chaos.

Thus, the translation of a particular genome (genotoken) into a particular phenome that either does or does not survive to reproduce is equivalent to the testing of a particular descriptive statement (a conceptual token) in a particular context. Either it survives the test or it does not. In biological evolution, each genome is an instance of a genotype. Indirectly, then, the genotype has been tested, albeit inadequately. However, especially in cases of sexual reproduction, each genotype is instantiated only by a single genotoken. One reason for narrowing one's focus in studying evolution to small segments of the genetic material is that they are more likely to have numerous copies. The same genotype is likely to have numerous genotokens to be tested in a variety of contexts. Thus, some estimation of the relative "worth" of this genotype can be gathered. Similarly, conceptual systems of considerable scope are extremely complex. It is very unlikely that more than one scientist adheres to precisely the same global conceptual system. In fact, a given scientist is unlikely to retain allegiance to the same global conceptual system for very long. Scientists change their minds. Global systems are tested only in the form of "versions." What makes something a "version" is not just similarity in structure. Descent is also required. Theories are best interpreted as families of models (Giere 1984), but these "families" have a necessary genealogical dimension. That the comparison just outlined is appropriate is indicated by the massive loss of information in both contexts and the messiness at the relevant interfaces. Only one small aspect of a scientific theory can be tested in a particular experimental setup, and the results can always be accommodated in a host of ways (in part because in any test too many concessions must be made to experimental contingencies). There are no absolutely crucial experiments.

In my discussion of both biological and conceptual evolution I have

emphasized the essential role of tokens ordered in lineages. The primary replicators in biological evolution are genotokens ordered into gene lineages. The primary replicators in conceptual evolution are conceptual tokens ordered in conceptual lineages. Is there no role for types—similar tokens regardless of descent? In biological evolution, there might well be. For example, albinism, eusociality, and photosynthesis apparently have each evolved numerous times. They are all tokens of the same type. From the point of view of phylogenetic descent, they are convergences—homoplasies rather than homologies. As such, their use in reconstructing phylogeny is likely to produce error. But there is more to evolutionary biology than phylogeny reconstruction. There is, for instance, the formulation of general statements concerning the evolutionary process, and one thing that is certain about the concepts incorporated in such general statements is that they must refer to types of phenomena. In this connection I do not think that either albinism or the ability to photosynthesize is a likely candidate for a type to function in general statements about the evolutionary process; eusociality and sexuality may be. If the concepts that function in statements of purported laws of nature are termed "natural kinds," then evolutionary biologists have not been tremendously successful in identifying natural kinds in the evolutionary process. One purpose of introducing such terms as replicator, interactor, and lineage is to specify class terms (types) more general than the traditional terms gene, organism, and species.

In the preceding discussion of the evolutionary process, terms such as replicator refer to types of entities. Anything anywhere that has the right characteristics counts as a replicator. It just so happens that included among these characteristics is temporal continuity. The entities themselves are historical entities; the type is not. However, when one moves to the level of conceptual evolution, replicator itself must be interpreted as a historical entity—a conceptual historical entity. As do all concepts, the term replicator has a history. Anyone who wants to understand the development of this concept must trace its history, and all the problems in distinguishing "homoplasies" and "homologies" arise. For example, Dawkins (1976) coined the term meme independent of Semon's (1904) earlier neologism. However, is there no role for type terms in our understanding of conceptual change? I think there is, just so long as one realizes that the instances of these type terms are themselves historical entities. To understand conceptual evolution, one must have a basic framework of conceptual historical entities. Periodically, a particular agent elaborates a set of conceptual entities in ways he or she takes to be genuinely general. These concepts will be evaluated as genuinely general (types with similar tokens), but in transmission this generality is lost once again. Only a few tokens actually get transmitted. The image that comes to mind is successive bursts of skyrockets. In each inflorescence, most of the rockets fizzle out; but a few

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explode into additional inflorescences, and so on (Hennig 1969, p. 43; Sneath and Sokal 1973, p. 321). Instead of treating the historically unrestricted types as constituting the general framework in which conceptual change is investigated, as is usually done, an evolutionary analysis takes a phylogenetic framework as basic; then conceptual types are periodically fitted into the interstices of this tree.

Numerous problems have been raised in connection with the testing of such conceptual systems as scientific theories that have nothing special to do with an evolutionary analysis as distinct from other analyses of conceptual change. However, one recurring problem that is particularly relevant concerns the social dimension of conceptual systems. Words do not confront the world in all their nakedness. Words do not mean anything. Instead, people mean things by the words that they use. In many semantic theories, people drop out and are replaced by an abstract relation between word and object or statement and state of affairs, a relation that ignores all characteristics of the actual meaning situation save the proposed isomorphisms. Omitting reference to the interaction in conceptual change leaves out not only the testing part of conceptual change but also the tester—in cases of science, the scientist.

As I have noted, both gene selectionists and organism selectionists find replication adequate to handle the bookkeeping aspect of biological evolution. If there is a "bookkeeping" aspect of conceptual change, it is embodied in simple changes in meme frequencies. Internalist historians of science are frequently chastised for leaving too much out of their histories of science, but even the most internalist historians include references to scientists in their histories. Scientists are the ones who devise and evaluate scientific theories. The relevant weakness of internalist histories is not that they omit reference to scientists but that they omit what is commonly termed the "social context" of science. However, one reason why many philosophers of science—among them Collins (1975), Bloor (1976), and Barnes (1977) feel uneasy about reference to "social context" is that they fear that it signals a relativist view of truth, and in many cases they are right. However, such references can also signal a relativist view of meaning. For example, Kitcher (1978) proposes to avoid some common semantic problems by postulating a community-based reference potential for each expression type. The reference potential of an expression type for a particular community is the "set of events such that production of tokens of that type by members of the community are normally instituted by an event in the associated set" (Kitcher 1978, p. 540).

Analyzing meaning in the context of communities of language users is certainly a step in the right direction for an evolutionary analysis of conceptual change, but several points must be emphasized. First, the communities must be defined by the appropriate relations, including such social relations as communicating with one another. If "reference potential" is to be of any use, communities cannot be defined in terms of their members' meaning the same things by the terms that they use. If communities are defined by the appropriate social relations, such as writes-to, reads-thepapers-of, and uses-the-work-of, one thing becomes clear: that plenty of conceptual heterogeneity exists in such communities (Hull 1984, 1985a). Instead of being a weakness, such heterogeneity is a strength. If biological evolution is to occur by selection, variability is necessary—both intra- and interspecific variability. If conceptual evolution is to occur by means of selection, both intra- and intercommunity variability must exist, and it does. One of the chief strengths of Kuhn's (1970) analysis of scientific change is that he views it as a community-based activity. One of its chief weaknesses is that he thinks that all scientists belonging to the same scientific community share the same "paradigm." As Kuhn (1970, p. 176) puts his position, "A paradigm is what the members of a scientific community share, and, conversely, a scientific community consists of men who share a paradigm."

Whether Kuhn intends for his "paradigms" in the preceding statement to be entire disciplinary matrices or particular exemplars (his two primary uses of the term paradigm), his position simply will not do. Because Kuhn portrays communities as monolithic entities, the transition from one paradigm to another seems a highly problematic affair—so problematic that some of Kuhn's readers have interpreted him as claiming that it is arational. Actually, all Kuhn has claimed is that simplistic analyses of rationality cannot explain such transitions. A community-based notion of rationality is more appropriate (Sarkar 1982). However, once one acknowledges that considerable differences of opinion can exist within any socially defined community, the radical differences in kind between intragroup and intergroup communication disappear. There is often as much intragroup dissonance (incommensurability) as intergroup dissonance. To the extent that incommensurability is a genuine problem at all, it is as much of a problem within scientific communities as between them (Hull 1985a). In the life of a community, cooperation is more important than agreement. It is a contingent truth that the scientists who make up the small, ephemeral research groups that are so operative in science can disagree with one another without ceasing to cooperate.

The crucial feature of an evolutionary analysis of conceptual change is that conceptual tokens be ordered into conceptual lineages. Because human beings are among the chief vehicles for conceptual replicators, there will be a significant, though not perfect, correlation between communities and such lineages. In order to understand conceptual change, in science as elsewhere, both social groups (such as the Darwinians) and conceptual systems (such as Darwinism) must be interpreted as historical entities (Hull 1985a).

Marjorie Grene, in an unpublished manuscript, has objected to certain hierarchical treatments of behavior because in them the "actor" in "interactor" drops out altogether. But if conceptual change is construed as community-based, actors play several crucial roles in it. Not only are the brains of human beings important vehicles (in Campbell's sense) in conceptual replication series, but human beings are equally important interactors (vehicles in Dawkins's sense). They are among the chief vehicles for conceptual replicators. They are also the entities that juxtapose scientific hypotheses and natural phenomena in experiments and observations. Conceptual replication and interaction intersect in human agents.

Human beings also participate in the social relations that integrate individual people into communities. Science is inherently and necessarily a community affair. Certainly isolated hermits can learn about the world, but if science had been constituted in its early years by such hermits it never would have gotten off the ground (Hull 1985b). In order for science to be cumulative (to the extent that it is), transmission is required. Similarly, the sort of objectivity and rationality that gives science the peculiar features that it has are characteristics not of isolated individuals but of individuals cooperating and competing in peculiarly organized social groups (Hull 1978b, 1985b).

Biologists commonly note that entities at different levels persist for different lengths of time. One constraining factor on group selection is that the organisms that compose groups come into being and pass away so much more rapidly than the groups of which they are temporarily part. With respect to calendar time, species speciate much more slowly than organisms reproduce themselves. Plotkin and Odling-Smee (1981) have extended this same observation to conceptual change. At each level in the relevant hierarchy, selection operates on a different time base. In this connection, the career lengths of particular scientists place some constraints on the speed of conceptual change. If we actually had to wait for aging scientists to die off before radically new ideas could become prevalent, this constraint would be prohibitive; however, no strong correlation seems to exist between age and the alacrity with which scientists adopt new ideas (Hull et al. 1978). Scientists change their minds on numerous issues during the course of their careers, but one thing is surely true: Whatever a scientist is going to accomplish, he or she must accomplish in the space of a very few decades. Just when scientists get really good at doing what they are doing, they die. Individual scientists exist for a long time relative to the speed of conceptual change, but not long enough to encompass certain sorts of conceptual change. This is but another reason why scientific communities are important. In a more global sense, it is the continuity of scientific communities through time that allows for continued scientific change.

I once entitled a paper on sociocultural evolution "The Naked Meme." I

ended that paper with the following cryptic observation: "If conceptual systems and their elements are interpreted as historical entities, actual transmission is essential, either directly from agent to agent in conversations or more indirectly through such means as the printed page. On the view being advocated by evolutionary epistemologists, conceptual evolution in the absence of social evolution leaves memes as naked as the apes who are their chief authors." (Hull 1982, p. 322) The main purpose of the present chapter has been to unpack this allusion by sketching the key role that actors play in section processes by emphasizing how important interaction is. Omitting interaction in characterizing biological evolution leaves out the causal relations that make replication differential. Including reference to such relations but terming the entities involved vehicles makes them sound much too passive. Perhaps replication alone is adequate to capture the "bookkeeping" aspect of biological and conceptual evolution; however, in the context of scientific change, omitting reference to interaction leaves out not only reference to testing but also reference to the entities keeping the books—scientists.

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Notes

- 1. Although Brandon (1982) and Sober (1984) agree that selection is a causal process, they disagree about which general analysis of causation can best handle selection adequately.
- 2. As much as Sober (1984) and Rosenberg (1985) disagree on other points, they agree that fitness is supervenient on the properties of individual organisms.

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Chapter 3

The Levels of Selection: A Hierarchy of Interactors Robert N. Brandon

Biologists have long recognized that the biosphere is hierarchically arranged. And at least since 1970 we have recognized that the abstract theory of evolution by natural selection can be applied to a number of elements within the biological hierarchy (Lewontin 1970). But what is it for selection to occur at a given level of biological organization? What is a "unit of selection"? Is there one privileged level at which selection always, or almost always, occurs? In this chapter I shall try to clarify and partially answer these questions.

Genotypes and Phenotypes

As Mayr (1978) has emphasized, evolution by natural selection is a twostep process. According to the received neo-Darwinian view, one step involves the selective discrimination of phenotypes. For instance, suppose there is directional selection for increased height in a population. That means that taller organisms tend to have greater reproductive success than shorter organisms. The reasons for this difference depend on the particular selective environment in which the organisms live. In one population it may be that taller plants receive more sunlight and so have more energy available for seed production; in another, taller animals may be more resistant to predation. Whatever the reason, natural selection requires that there be phenotypic variation (in this case, variation in height). Selection can be thought of as an interaction between phenotype and environment that results in differential reproduction.

But natural selection in the above sense (what quantitative geneticists call phenotypic selection) is not sufficient to produce evolutionary change. In the case of directional selection for increased height, selection may change the phenotypic distribution in the parental generation (it will do so if selection is by differential mortality); but whether or not that results in evolutionary changes, (i.e., changes in the next generation) depends on the heritability of height. That is, it depends on whether or not taller-thanaverage parents tend to produce taller-than-average offspring and shorter-