INDIVIDUALITY ♦4180
AND SELECTION

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Evolutionary theory is currently undergoing a period of rapid development,
but in the process several problems have cropped up that are proving to be
infuriatingly difficult to resolve—e.g. the presence of so much genetic
heterogeneity in natural populations, the prevalence of sexual forms of
reproduction in the face of an apparent 50% cost of meiosis, and the
difficulty of explaining how selection can operate at higher levels of orga-
nization. In their most recent publications, the leading theoretical biologists
of our day seem to have all but given up hope of making further progress
(28, 34, 58). Comparable stalemates in the history of science have tended
to result from everyone concerned taking for granted something so funda-
mental that no one in their right mind would question it. In the present case,
I think two assumptions are at fault: (*a*) the view that genes and organisms
are "individuals" while populations and species are "classes," and (*b*) our
traditional way of organizing phenomena into a hierarchy of genes, cells,
organisms, kinship groups, populations, species, and ecosystems or commu-
nities.

In his classic paper on units of selection, Lewontin (27) accepts the
traditional organizational hierarchy and asks at what level selection can
occur. His answer is that it takes place primarily at the lower levels and
becomes rarer and more problematic at the higher levels. However, some-
thing peculiar happens as we follow Lewontin up the traditional hierarchy:
We pass from such commonsense individuals as genes and organisms,
through such borderline cases as colonies, to such commonsense groups as
populations and species. It would be truly amazing if a single process could
operate on entities as different as individuals and groups. At least some of

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the difficulty in specifying the conditions under which group selection can occur arises from the lack of a sufficiently careful statement of how "individuals" differ from "groups" and of how these differences bear on selection.

From the beginning of the controversy over group selection, two quite different sorts of "groups" seem to have been intended: highly organized groups exhibiting group characteristics and organisms that happen to be located in close proximity to each other. In his classic statement, Wynne-Edwards (64) seems to have had the first sort of group in mind. For example, he says, "In developing the theme it soon became apparent that the greatest benefits of sociality arise from its capacity to override the advantage of the individual members in the interests of the survival of the group as a whole. The kind of adaptations which make this possible, as explained more fully here, belong to and characterize social groups as entities, rather than their members individually. This in turn seems to entail that natural selection has occurred between social groups as evolutionary units in their own right. . . ."

The controversy over group selection has taken two unfortunate turns. First, Wynne-Edwards himself chose about the least likely group characteristic to investigate—the regulation of population size by altruistic restraint. That the selection of one sort of group trait is difficult or impossible does not demonstrate that other sorts of group characteristics cannot be selected. Second, both critics and defenders of group selection have tended to ignore the sort of groups Wynne-Edwards had in mind and to concentrate on organisms that form groups only because they happen to live on the same host or in the same pond (27, 51, 56, 57, 59). In this paper I intend to do just the opposite. Most biologists seem to take for granted that organisms can be selected. In fact, organisms are the primary focus of selection (1, 15, 27, 36, 41). Can entities more inclusive than organisms be selected in the same sense that organisms can?

Such critics of group selection as Williams (56, 58) assume that organisms can be selected and then argue that more inclusive entities cannot be selected because they lack certain characteristics. Such critics of organism selection as Dawkins (6, 7) respond that not even organisms can be selected because they too lack these characteristics. Thus, biologists are presented with a dilemma. If the arguments against the selection of such "groups" as colonies and populations are cogent, then organisms cannot be selected either. However, any relaxation of standards sufficient to allow organisms to be selected permits entities more inclusive than organisms to be selected as well.

In his treatment of the subject, Lewontin (27) begins with a brief characterization of the evolutionary process and then proceeds to review evidence for and against the operation of selection at various levels of organization. I propose to do the opposite, to investigate the general characteristics of the

evolutionary process at some length and then to discuss only briefly the particular entities that may or may not possess the characteristics necessary to function in this process. I contend that group selection of the sort Wynne-Edwards had in mind is not just rare, it is impossible. Anything that has the characteristics necessary to be selected in the same sense in which organisms are selected has the characteristics necessary to count as an individual and not a group. Not all individuals can function as units of selection, but only individuals can be selected. However, many entities commonly treated as groups are actually individuals.

Individuals and Groups

The preceding claims sound more extreme than they are because of a systematic ambiguity in the term "individual." It is used sometimes in a narrow sense to mean "organism," sometimes in a broader sense to denote any spatiotemporally localized and well-integrated entity, such as a gene or a cell (24). Thus Wilson (60) is forced to call colonies "superorganisms" when he attempts to show that they can function as units of selection, as is Dobzhansky (9) when he makes comparable claims about species. Similarly, both gene selectionists and organism selectionists call themselves "individual selectionists" and complain that others consider kin selection an example of group selection when it is actually an instance of individual selection (7, 27, 56, 62). Although the controversy over group selection is not merely terminological, such terminological complexities do not help. In this paper, I use "individual" as a generic term in contrast with "group" and "class."

Individuals are spatiotemporally localized entities that have reasonably sharp beginnings and endings in time. Some individuals do not change much during the course of their existence, others undergo considerable though limited change, and still others can change indefinitely until they eventually cease to exist. But regardless of the change that may occur, the entity must exist continuously through time and maintain its internal organization. How continuous the development, how sharp the beginnings and endings, and how well-integrated the entity must be are determined by the processes in which these individuals function, not by the contingencies of human perception. It is only an accident of our relative size, longevity, and perceptual acuity that we can see the distances between the organisms that comprise a species but not the even greater relative distances that separate the atoms that make up an organism (16, 24, 25). For long enough we have remained, to use Gould's (17) phrase, "prisoners of the perceptions of our size."

The elements that comprise an individual do so because of how they are organized and not because of any shared similarity (16, 24, 25). For example, the cells that comprise an organism tend to be genetically identical, but

this is not why they all belong to the same organism. At one extreme, the cells of a gynandromorph are genetically quite different yet belong to a single organism, while at the other extreme, the cells of identical twins belong to different organisms even though they are genetically identical. Although many individuals are functionally organized systems, many are not—e.g. an atom of gold. Nor are the relations that can organize parts into a whole exclusively spatiotemporal. For example, even though its parts may not be contiguous, an operon functions as a whole in the production of proteins. The distinction between structural and functional wholes is important because opponents of group selection tend to recognize only structural wholes.

Philosophers use the term "class" in a very general sense (30). Classes are the sorts of things that can have members, and entities are considered members of a class because they possess certain properties. For example, planets are relatively large, nonluminous bodies revolving around stars. Classes of the sort that function in scientific laws must in addition be spatiotemporally unrestricted (24, 25). The term "group" as biologists use it is halfway between individuals and classes. Groups tend to be spatiotemporally localized and their members considered part of the group because of their location and not because of any internal organization. Selection can act only on spatiotemporally localized entities, but if it is to act on entities more inclusive than organisms in the same sense in which it acts on organisms, these entities must be cohesive wholes and not classes or groups. An individual can be selected for the properties it exhibits. A group can be selected only incidentally—e.g. because all its members happen to be in close proximity to each other. Finally, a genuine class can be selected only via its members. Wilson (61) puts the issue as follows: "In zoology the very word colony implies that the members of the society are physically united, or differentiated into reproductive and sterile castes, or both. When both conditions exist to an advanced degree, as they do in many of these animals, the society can equally well be viewed as a superorganism or even as an organism. The dilemma can therefore be expressed as follows: At what point does a society become so well integrated that it is no longer a society?"

Thus the first thing a biologist does in arguing that an entity can or cannot function as a unit of selection is to argue that it is or is not an individual. For example, gene selectionists such as Dawkins (6, 7) contend that in most cases entire genomes cannot function as units of selection because they are "torn to smithereens" at meiosis. Organism selectionists such as Mayr (39) disagree. "The genes are not the units of evolution nor are they, as such, the targets of natural selection. Rather, genes are tied together into balanced adaptive complexes." Genes are "linked" both structurally on chromosomes and functionally in biosynthetic pathways. As structural wholes, they

are rearranged to some extent at meiosis. Nevertheless, even in the face of such structural rearrangement, genomes can remain functional wholes (63).

Even though biologists disagree about which entities possess the necessary characteristics to be selected, even though they disagree whether these entities must be structural or functional wholes, they agree that they must be individuals. For example, Dawkins (6) and Eldredge & Gould (11) occupy opposite poles in the selectionists' controversy. They agree that organisms, populations, and species are the same sort of thing, but they disagree about what sort. Dawkins argues that from the point of view of selection, they are all amorphous aggregates, as ephemeral as "clouds in the sky or dust-storms in the desert," while Eldredge & Gould contend that they are all homeostatic systems, "amazingly well-buffered to resist change and maintain stability in the face of disturbing influences."

In this paper I am concerned not so much with deciding which entities have the characteristics necessary to function in the evolutionary process as with specifying the precise nature of these general characteristics. To do this I distinguish between three distinct but interrelated processes—replication, interaction, and evolution. Certain entities (replicators) pass on their structure largely intact from generation to generation. These entities either interact with their environments in such a way as to bias their distribution in later generations or else produce more inclusive entities that do. As a result, even more inclusive entities evolve.

Levels of Selection

The living world is traditionally divided into a hierarchy of organizational levels: genes, cells, organisms, colonies, populations, species, and ecosystems or communities. Not all levels are exhibited in every instance. For example, not all genes exist in cells, nor in unproblematic organisms. Only a small percentage of organisms form colonies. Depending on how one defines "population" and "species," some organisms form populations and species; others do not. If gene exchange is necessary, then the vast majority of organisms form neither populations nor species but only clones. When the organic world is conceptualized traditionally, individuality wanders from level to level, and as it does, so too does the level at which selection can occur.

Even such enthusiastic gene selectionists as Dawkins (6, 7) admit that the *amount* of genetic material being selected at any one time can vary. In genetically heterogeneous populations of sexual organisms, only single genes last long enough to be selected; but in cases of strictly asexual reproduction, the entire genome can function as a unit of selection. Organism selectionists acknowledge that selection can operate differently at different stages in the life cycle of an organism—e.g. the larvae may be pelagic and

the adults sessile. But what if an organism changes from an individual to a group and back to an individual again during the course of its life cycle the way that certain slime molds do (2, 50)? Oster & Wilson (43) reply that, as the entities change from individuals to groups, the focus of selection shifts. For example, early in the development of a hive in a particular species of bee, selection occurs at the organismic level because of the presence of several queens, but after the number of queens has been reduced to one, selection operates at the level of the hive. Similarly, advocates of species selection do not maintain that all species in all circumstances can be selected, but only that some can in certain circumstances. Finally, when biologists such as Dunbar (10) argue that "selection may apply at the level of the ecosystem as well as at the levels of the individual and the specific population," they do not contend that all ecosystems can function as units of selection but only that mature ecosystems in the warmer latitudes can.

When biologists address the issue of the levels at which selection can occur, they take the traditional organizational hierarchy as fundamental and the level at which selection operates as variable. As a result, selection wanders from one level to the next from time to time and from group to group, sometimes acting on genes, sometimes organisms, sometimes colonies, etc. As long as the traditional hierarchy is taken as basic and the levels at which selection can occur as variable, no simple, nomothetic generalizations are likely to materialize. Rather, the evolutionary process must be taken as basic and the levels defined in terms of it. Two entities that perform the same function in the evolutionary process must be classed as the same sort of entity even if one happens to be an organism and the other a colony or a population. In his book on insect societies, Wilson (60) argues that organisms and colonies should be treated as the same sort of thing because they play the same role in the evolutionary process.

Hamilton (20) complains that Ghiselin's (15) views on altruism force him to say, "in effect, that a 'family' or 'breeding stock' is the equivalent of an individual. Maybe in some sense it can be *almost* equivalent; nevertheless, it seems to me both more exact and less 'metaphysical' to stick to common usage." Likewise the reconceptualizations suggested in this paper may seem too metaphysical, too radical—as radical and metaphysical as those introduced into physics a half century ago. With the work of Einstein, physicists were faced with a dilemma: If they insisted on retaining Euclidean geometry, they would have to be content with extremely complicated and variable laws; if they wanted laws applicable anywhere in the universe, regardless of velocity, they would have to abandon Euclidean geometry. They opted for the second alternative. Evolutionary biologists are currently confronted by a similar dilemma: If they insist on formulating evolutionary theory in terms of commonsense entities, the resulting laws are likely to remain

extremely variable and complicated; if they want simple laws, equally applicable to all entities of a particular sort, they must abandon their traditional ontology. This reconceptualization of the evolutionary process is certainly counter-intuitive; its only justification is the increased scope, consistency, and power of the theory that results. If the terminology suggested in this paper cannot characterize the evolutionary process more accurately and succinctly than the traditional terminology, it should not (and will not) be adopted.

Replicators and Interactors

As Mayr (41) emphasizes, "Evolution through natural selection is (I repeat!) a two-step process." He describes the process in terms of genetic variability and the ordering of that variability by selection. Here I will define the units functioning in these two processes in terms of their most general characteristics; I leave open the question of which entities perform these functions. Building on the work of Williams (56), Dawkins (7) suggests *replicator* as a general term for the entities that function as units of selection, regardless of what these entities turn out to be. "Why 'replicator selection' rather than 'gene selection'?" Dawkins (7) asks. Because it does not prejudge the empirical issues. "The term replicator should be understood to *include* genetic replicators, but not to exclude any entity in the universe which qualifies under the criteria listed."

These general criteria are longevity, fecundity, and fidelity. All three characterize individuals functioning in a copying process. Replicators need not last forever. They need only last long enough to produce additional replicators that retain their structure largely intact. The relevant longevity concerns the retention of structure through descent. Some entities, though structurally similar, are not copies because they are not related by descent. For example, although atoms of gold are structurally similar, they are not copies of one another because atoms of gold do not give rise to other atoms of gold. Conversely, a large molecule can break down into successively smaller molecules as its quaternary, tertiary, and secondary bonds are severed. Although descent is present, these successively smaller molecules cannot count as copies because they lack the requisite structural similarity. Replication by itself is sufficient for evolution of sorts, but not evolution through natural selection. In addition, certain entities must interact causally with their environments in such a way as to bias their distribution in later generations. Originally, these two functions may have been performed by the same entities. The original replicators may well have replicated themselves and interacted with their environments in such a way as to bias their distribution in later generations. But because these two processes are inherently such different processes, requiring very different properties, they

eventually became separated into different individuals at different levels of organization. Replicators not only replicate themselves but also produce other entities that interact with ever more inclusive environments.

When Dawkins (7) defines "replicator," he has replicators interacting with their environments in two ways—to produce copies of themselves and to influence their own survival and the survival of their copies. Just as Dawkins coined the term "replicator" for the entities that function in the first process, I (26) have suggested "interactor" for the entities that function in the second process. Why "interactor" rather than "organism?" For the same reason Dawkins substituted "replicator" for "gene." Just as genes are not the only replicators, organisms are not the only interactors. Thus, the two sorts of entities that function in selection processes can be defined as follows:

replicator: an entity that passes on its structure directly in replication

interactor: an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential

With the aid of these two technical terms, the selection process itself can be defined:

selection: a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them

Thus the question of the levels at which selection takes place must be divided into two questions—at what levels does replication occur, and at what levels does interaction occur? If an entity is to function as a replicator, it must have a structure and be able to pass this structure on to successive generations of replicators. As a replicator it need interact with its environment only to the extent necessary to replicate itself. Although replicators may be part of functional systems, they themselves need not be functional systems. The only adaptations they need exhibit are those to promote replication. For example, a gene as a stretch of DNA is adapted to replicate itself. It may "code" for other adaptations but does not itself exhibit these adaptations.

Interactors must exhibit structure but toward quite different ends—they must be able to cope with their environments. The "success" of an interactor is *measured* in terms of differential perpetuation of the replicators it produces, but it can be *defined* in such terms only at the price of greatly reducing the empirical content of evolutionary theory (17, 29, 56). To be sure, the desire to insulate evolutionary theory against falsification by defining "fitness" solely in terms of differential replication is understandable, as

understandable as the tendency of behavioral psychologists to define "intelligence" solely in terms of scores on IQ tests, but it must be resisted for exactly the same reasons. Instead, some sort of reference must be made to various "engineering" criteria of fitness (17). For example, one way of maintaining a constant internal temperature in the face of variation in external temperature is the production of a layer of insulation, whether fur, feathers, blubber, or something else. As difficult as it is to apply such engineering criteria of fitness in particular cases, I see no way in which such difficulties can be circumvented without evolutionary theory degenerating into an empirically empty formalism.

Dawkins (6, 7) defines "replicator" in terms of strict identity in structure. A change in a single base pair results in a new replicator. According to Dawkins, nothing more inclusive than a genome in asexual organisms and small segments of DNA in sexual organisms can count as replicators. Certainly organisms cannot. Because of the role of the environment in development, even identical twins are likely to differ. In my definition, a replicator need only pass on its structure largely intact. Thus entities more inclusive than genomes might be able to function as replicators. As I argue later, they seldom if ever do. The relevant factor is not retention of structure but the directness of transmission. Replicators replicate themselves directly but interact with increasingly inclusive environments only indirectly. Interactors interact with their effective environments directly but usually replicate themselves only indirectly.

As simple as the distinction between replication and interaction is, it goes a long way toward resolving certain apparent disagreements that characterize the biological literature. For example, Ayala (1) notes that "it must be remembered that each locus is not subject to selection separate from the others, so that thousands of selective processes would be summed as if they were individual events. The entire individual organism, not the chromosomal locus is the unit of selection, and the alleles at different loci interact in complex ways to yield the final product."

Dawkins (7) disagrees. "Of course it is true that the phenotypic effect of a gene is a meaningless concept outside the context of many, or even all, of the other genes in the genome. Yet, however complex and intricate the organism may be, however much we may agree that the organism is a unit of *function,* I still think it misleading to call it a unit of *selection.* Genes may interact, even 'blend', in their effects on embryonic development, as much as you please. But they do not blend when it comes to being passed on to future generations."

At the very least, Ayala claims that organisms are interactors. Maybe so, Dawkins responds, but they are not replicators. Evolution of sorts could result from replication alone, but evolution through natural selection re-

quires an interplay between replication and interaction. Both processes are necessary. Neither process by itself is sufficient. Omitting reference to replication leaves out the mechanism by which structure is passed from one generation to the next. Omitting reference to the causal mechanisms that bias the distribution of replicators reduces the evolutionary process to the "gavotte of the chromosomes," to use Hamilton's (20) propitious phrase. The simplicity of a theory of evolution couched entirely in terms of changes in replicator frequencies is purchased at the price of drastically reduced empirical content.

Levels of Replication

In order for an entity to function as a replicator, it must have structure and be able to pass on that structure—the more directly the better, the more intact the better. When replication is described in this way, genes are obviously the most fundamental replicators. However, biologists sometimes reject other entities as replicators because they lack certain characteristics, characteristics that even genes do not possess. For example, Stern (47) complains that the "theory of natural selection offers no conclusion that could tell us what it means for an individual to be selected. In the 'eyes' of selection, organisms are merely temporary carriers of characteristics. Individuals die, they are neither preserved nor increased in frequency, and therefore are not selected." Similarly, Williams (56) claims that his view of selection "necessitates the immediate rejection of the importance of certain kinds of selection. The natural selection of phenotypes cannot in itself produce cumulative change because phenotypes are extremely temporary manifestations." However, if this line of reasoning were cogent, it would count just as strongly against genes as against organisms. Neither genes nor organisms are preserved or increased in frequency. The phenotypic characteristics of organisms are extremely temporary manifestations—almost as temporary as the "phenotypic" characteristics of genes. As substantial entities, all replicators come into existence and pass away. Only their structure persists, and that is all that is needed for them to function as replicators.

Genes and Genomes

Genes are "linked" both structurally in chromosomes and functionally in biosynthetic pathways. Can chromosomes or possibly entire genomes function as replicators? If not, can they be considered functional wholes? Lewontin (27) begins his discussion of individual selection by claiming that the "primary focus of evolution by natural selection is the individual" and then immediately launches into a discussion of the genotype. To be sure, there is a one-to-one correspondence between genotypes and organisms, but the structural unity of the genotype and the functional unity of the genotype

in the production of the organism must be kept distinct from each other and from the "unity of the organism."

In asexual reproduction, the structure of the entire genome is transmitted. In sexual reproduction, there is always the danger of recombination. Recombination has no effect on the structure of genomes in genetically homogeneous populations. However, the more heterogeneous a population is, the more likely that the structure of genomes will be altered by crossover during meiosis. How much alteration can occur before a genome must be considered a new replicator depends on the effect the changes have on the organism as an interactor. How similar is similar enough? Similar enough to respond similarly to similar selection pressures (56). Before turning to this topic, one consequence of this line of reasoning must be mentioned. Small populations tend toward increased homogeneity, both because a very few organisms cannot possibly incorporate all the genetic heterogeneity of a large population and because of the effect of inbreeding. If speciation occurs always or usually by means of small, peripheral isolates (11, 18, 36, 39), then at speciation, when it really counts, entire genomes can function as replicators.

When the "unity of the genotype" is appealed to, functional unity is usually at issue. If genotypes are functionally organized wholes, it is difficult to see how their constituent parts could be rearranged much without significant disruption of function. Surprisingly, the evidence for the expected linkage disequilibrium is currently equivocal (13). However, from the point of view of replication, structural unity is what matters, not functional unity. (Functional unity is discussed in the next section in connection with interaction.)

Organisms and Colonies

In asexual reproduction, the entire organism can replicate, albeit in conjunction with the genetic material. In such cases, these organisms are as much replicators as are genes. Sexual reproduction is quite another matter. The only structure literally transmitted from parent to offspring is the structure of the genetic material. At the very least, replication at the level of sexual organisms is indirect, one place removed from the genetic material. How much structural similarity is present in organism lineages? Obviously, in genetically homogeneous populations, ancestor-descendant sequences of organisms consist of individuals that are structurally quite similar: variation is introduced only by environmental differences. Even in genetically heterogeneous populations of sexual organisms, organisms need not vary greatly from generation to generation. Much of the genetic heterogeneity present in populations has little or no phenotypic effect. The functional unity of the genotype in the production of organisms promotes

the structural similarity of organisms. To the extent that variation in the overall structure of organisms is selectively neutral, organisms can function as replicators, keeping in mind that the transmission of structure is not as direct as in asexual reproduction.

In order for colonies to function as replicators, they must be individuals, possess structure of their own, and be able to pass on this structure largely intact. Although Wilson (59) admits that the "insect society is a decidedly more open system than the lower units of biological organization such as the organism and the cell," he still maintains that colonies can function as units of selection. The "great innovation" in the evolution of social insects was the "reproductive neuter, which fixed the limits on the amount of caste differentiation that could occur among the colony members." If ants are *part* of their colony, then they need be no more alike than are the cells that make up an organism. Epithelial and liver cells differ as much as do worker and soldier ants.

In some cases at least, colonies seem to have all the gross characteristics of organisms. Their boundaries are frequently distinct. They exhibit internal differentiation and division of labor. They have properties of their own— e.g. the percentage of organisms in each caste and the distribution of these castes throughout the colony. Colonies are even capable of passing on these properties when they reproduce themselves: Sometimes a single colony splits equitably into two; sometimes only one or several organisms leave the parent colony. However, as Lewontin (27) has pointed out, all the cells in an organism in most cases contain the same genes, while "sterile diploid workers are not genetically identical with the fertile queen or the fertile haploid males." Thus, sexual reproduction presents the same range of problems for colonies functioning as replicators as it does for organisms.

Populations and Species

It is difficult to tell whether any of the biologists who argue for population selection have replication in mind. Because they mention "population structure," they might. In the preceding discussion, I did not bother to argue that genes, organisms, and colonies are individuals that exhibit structures of their own. In the case of populations, these characteristics cannot be taken for granted. For example, Lewontin (27) distinguishes between kin selection and the differential survival and reproduction of a population: "Survival of such a unit means simply that the entire population has not become extinct, regardless of the numbers of individuals it contains. Reproduction of a population is more difficult to define, but since we are concerned with some property of the population, then reproduction must mean the budding off of new colonies with the same characteristic property whose evolution we are explaining."

If populations are to function as replicators, they must be able to "replicate" themselves, either by splitting equitably into two or more populations or by sending out a few organisms to start new populations. Most populations are genetically quite heterogeneous. A population might retain its characteristic gene frequencies if splitting occurs, but the populations that result from a few colonizers are likely to be genetically quite different from the parent population. Furthermore, in what sense can populations be said to have "structure?" As we have seen, organisms and colonies are functional wholes. They also exhibit structural characteristics. Whether or not they can transmit this structure with sufficient regularity and fidelity to function as replicators is less clear. Stehr (46) argues that populations are both functional and structural wholes: "One of the basic concepts in population biology is obviously the concept of population itself. The term population often evokes a numerical, merely quantitative, image. Too many ecologists still use the term 'population' as if it would refer to a smaller or larger number of similar individuals, the key words being 'number' and 'similar.' But this is false and the opposite is true. Population is a functional and structural term referring to an integrated grouping of dissimilar and, therefore, mutually dependent individuals."

A continuing feud exists between traditional evolutionary biologists and practitioners of what they deride as "beanbag genetics" (19, 35, 36, 37, 39, 42). The main point of contention is the existence and adequate treatment of levels of organization more inclusive than single genes. Can properties of structured wholes be reduced without loss to the properties of their parts (63)? Although this question tends to crop up in the context of population selection, it is equally relevant at all levels of organization. The mass of an organism is nothing but a simple summation of the masses of its parts. A certain percentage of cells will be nerve cells, a certain percentage liver cells, etc. But organism selectionists argue that of greater importance is the distribution of these cells throughout the organism. One cannot understand the role organisms play in the evolutionary process if their structure is ignored. Similarly, the mass of a particular hive of bees is nothing but a simple summation of the masses of its parts. A certain percentage of bees will gather food, a certain percentage circulate air in the hive, etc. But colony selectionists argue that of greater importance is the distribution of these organisms throughout the hive.

Gene selectionists seem to think that all this higher level organization can be ignored without loss. The only organization that matters is the order of bases in DNA. But a physicist might argue that the mass of a gene is nothing but a simple summation of the masses of its constituent parts. A certain percentage of these parts contain guanine, a certain percentage adenine, etc. But gene selectionists are sure to complain that of greater importance is the

order of bases in the molecule. Hence, one issue that divides biologists is the levels at which organization must be acknowledged in the evolutionary process. One problem they all share, however, is the nature of organization itself and what role it plays. With respect to populations, the chief problem is the locus of population structure. It is certainly true that populations are spatiotemporally localized entities that develop continuously through time. Gene exchange also serves to promote internal cohesion. Thus, populations are reasonably good examples of individuals; but to function as replicators, they must be special sorts of individuals. They must exhibit structure of their own and be able to pass it on. At times population structure is treated as if it followed from the unity of the genotype. Because all organisms that makeup a population share the same core elements in their genotypes, the population itself is supposedly in some sense a "whole." At the very least, the notion of population structure needs considerable elucidation. As it stands, it remains problematic.

These problems are only magnified at the level of entire species. Although some species of sexual organisms are made up of a single population, most include several populations that are at least periodically disjunct. As long as the constituent populations exchange an occasional organism, such species can be considered a single, integrated individual. However, when populations remain totally disjunct for long periods ("long" in evolutionary terms), some other criterion must be discovered for including them in the same species. That these populations remain potentially interbreeding means that they are potentially a single individual. The commonest objection raised to potential interbreeding as a criterion for species status has concerned its operational applicability. Such operationist objections to one side (22), the real problem is its relevance. Two drops of mercury might be potentially one. If they came into contact with each other, they might merge into a single drop. However, until they do, they remain two drops and not one. Comparable observations should hold for populations as parts of a single species. Do claims of reproductive isolation concern the structure of the species as a whole, its constituent populations, or the genomes of the separate organisms? Eldredge & Gould (11) claim that species are homeostatic systems, but they are not very explicit about the actual mechanisms that produce this homeostasis. However, one point should be noted: If species and populations are structured wholes, genetic heterogeneity is no longer problematic. One expects individuals to be made up of varied parts.

In sum, replication seems concentrated at the lower levels of the organizational hierarchy, occurring usually at the level of the genetic material, sometimes at the level of organisms and possibly colonies, but rarely higher.

Levels of Interaction

Genes, cells, and organisms all interact with their respective environments in ways that result in differential replication. They are organized wholes that exhibit properties of their own, and the nature of these properties determines their success as interactors. In most cases when biologists argue that entities more inclusive than single genes function in the evolutionary process, they have interaction in mind, not replication. For example, Emerson (12) argues that colonies must develop adaptations analogous to the adaptations of individual organisms if colonies are to be the sorts of thing that can be selected. Wilson (60) maintains that the "superficial aspects of caste, communication, and other social phenomena represent adaptations that are fixed by natural selection at the colony level." To be sure, the reproductives that transmit the gametes are the "ultimate focus of selection," but "it remains true that the colony is selected as a whole, and its members contribute to colony fitness rather than individual fitness."

Similarly, Williams (56) argues that herds of ungulates cannot be selected because they lack any significant specialization. However, if such specializations were present, that "would justify recognizing the herd as an adaptively organized entity." He goes on to argue, "Unlike individual fleetness, such group-related adaptations would require something more than the natural selection of alternative alleles as an explanation." If herds are, as Williams claims, not functionally organized systems, then they would have no adaptations to explain in the first place, whether by alternative alleles or anything else. The issue is whether entities more inclusive than organisms exhibit adaptations and, if so, whether they can be explained by reference solely to alternative alleles. For those biologists who think no reference need be made in evolutionary explanations to organisms as interactors, the question never arises. If organisms need not be mentioned, certainly higher level interactors can be ignored. However, those biologists who believe that the process I have named "interaction" is central to the evolutionary process must address the question, Can entities more inclusive than organisms function as interactors?

Colonies seem clear examples of interactors. They are organized wholes. Individual organisms do not confront their environments in isolation but as parts of larger wholes. Populations and species once again pose special problems. The problem is not genetic heterogeneity, the retention of structure, and the like. These are characteristics of replicators, not interactors. The problem is the existence of populational adaptations, properties characteristic of the population as a whole that allow it to interact with its environment as a whole. If populations and/or species are homeostatic systems, then some such properties must exist. If populations and possibly

entire species are to function as interactors, it is not enough that they be made up of homeostatic systems; they themselves must exhibit the appropriate characteristics. Once again, a greater specification of these properties is necessary before any reasonable decision can be made on the issue.

Previously I made the blanket claim that "group selection" is impossible because in order to be selected in the sense investigated in this paper an entity must be an individual. Anything that can be selected the way an organism can, must be the same sort of thing an organism is. Most discussions of group selection concern the selection of groups just because all the members of the group happen to be confined to the same locality, either because of some barrier or because of population viscosity (51, 57, 59). Such groups are genuine groups, and this sort of selection is genuine "group" selection of the sort that requires such special circumstances (27). More recently, Stanley (45) has argued for a process he terms "species selection," a process that differs both from interaction at levels more inclusive than organisms and from genuine group selection, because it does not explain the origin of adaptations. Rather, species selection determines the "fate of adaptations, once established." In Stanley's view, species are neither replicators nor interactors (see also 48).

When biologists refer to the occurrence of selection at levels "higher" than species, they usually have in mind not higher taxa but ecosystems or communities. I did not discuss ecosystems and communities in connection with replication because no one seems to have argued that these systems can function as replicators. If anything, they can function as interactors. According to Hoffman (21), "The basic assumption of community ecology and paleoecology is that the recurrent species associations which comprise ecological communities or biocenoses represent a distinct level of biotic organization achieved through ecological integration and coevolution among the species. Under this assumption, communities are claimed to be real biological units each of which is defined by its particular taxonomic composition and ecological structure."

Ecological communities certainly give every appearance of being functionally organized systems, much more so than particular species. The major stumbling block in the path of treating such systems as interactors is the independence of their constituent replicators. All of the examples of interactors discussed thus far have contained as part of their own make-up a single set of replicators. Even if higher-level entities can function on occasion as replicators, the most fundamental replicators in every case are genes. The success or failure of an organism in reproducing itself affects the replication of its genes, *all* its genes. The organisms that comprise an ecological community may interact with the environment of the community

as a cohesive whole, but the effects of these interactions on their constituent replicators are not unitary. Hoffman (21) concludes that there is "no intrinsic, biotic mechanism inducing community dynamics that is an inherent trend to maximize a selection value in either ecological, or evolutionary time." At the very least, ecological communities are extremely problematic interactors.

In sum, entities function as interactors at higher levels of organization than those at which replication occurs, at least at the level of colonies, possibly at the level of populations, but probably at no higher levels.

Lineages

Replicators and interactors are the entities that function *in* the evolutionary process. Other entities evolve *as a result* of this process, entities commonly termed species. However, the main strategy of this paper is to select terms that are neutral with respect to the empirical points at issue and to define these terms so that any entity possessing the appropriate characteristics can count as performing that function. In this instance, there is no need to invent a term. One is already available:

> *lineage:* an entity that changes indefinitely through time as a result of replication and interaction

Neither genes nor organisms can function as lineages because neither can change indefinitely without becoming numerically distinct individuals. However, both form lineages that can and do evolve. In asexual organisms the gene lineages are contained wholly within organism lineages and form constantly branching trees. Recombination at meiosis in sexual organisms has two results: Gene lineages do not form trees but networks, and the structure of the genetic material is altered to some extent from generation to generation even in the absence of mutation. Thus, in sexual organisms, the limits of gene-lineages expand to the limits of the gene pool, while the limits of single replicators gradually shrink to the single nucleotide through successive replications.

On the usual view, species change indefinitely through time and hence are paradigm lineages. But according to Eldredge & Gould (11, 18), most species cannot change much during the course of their existence. Thus, they cannot evolve. However, like genes and organisms, they form lineages, and these lineages evolve. In the vast majority of animal species, species (or species-lineages) form constantly branching trees. In plants, they continue to anastomose. Eventually, however, even plant species form trees. An important characteristic of lineages is that each lower-level lineage is included as part of all subsequent higher-level lineages. Gene-lineages are included physically as part of organism-lineages. Assuming that these or-

ganisms in turn form colonies, the relevant organism-lineages are included in colony-lineages, and so on, up to the level of biological species.

Those biologists who attempt to characterize the species category as an evolutionary unit emphasize *coherence* and *continuity,* two of the most important characteristics of individuals (16, 38, 44, 49, 53). As Mayr (38) summarizes this position, "Uniquely different individuals are organized into interbreeding populations and into species. All the members are 'parts' of the species, since they are derived from and contribute to a single gene pool. The population or species as a whole is itself the 'individual' that undergoes evolution; it is not a class with members" (see also 40). Recent authors who argue that species are individuals do not claim that species are replicators or interactors, though they might be, but that they are the entities that evolve as a result of the interplay between replication and interaction. They are lineages. More than that, they are the most inclusive entities that are "actively evolving entities," to use Wiley's (54) phrase. According to Wiley, "supraspecific taxa are not actively evolving entities and thus cannot 'give rise' to anything. Put briefly, once a species speciates, it is no longer a single evolving lineage but a series of separate and independently evolving groups." Species are certainly part of the sections of the phylogenetic tree commonly designated as higher taxa, but these taxa evolve only as a result of the evolution of their constituent species.

Comparable observations hold for the lineages formed in asexual reproduction. Advocates of the biological species concept (9, 38) have long claimed that strictly asexual organisms do not form species, an assertion that has seemed overly chauvinistic to some. However, the point is that strictly asexual organisms form no higher-level entities; organism-lineages are the highest-level lineages produced (48). They alone evolve as a result of replication and interaction. Just as not all organisms form colonies, there is no reason to expect all organisms to form species (49). Or put in the opposite way, these organism-lineages *are* the species in asexual organisms.

Cook (5) makes comparable distinctions with respect to clonal development in plants. He terms each physiological unit a "ramet" and the entire clone a "genet." He then concludes that "it is the genet upon which natural selection operates. In a large, widespread clone the death of a ramet may have as little evolutionary consequence as the pruning of a branch from a large tree or the loss of a leg in an insect." Cook's observations are appropriate to genets that retain physical connections between their parts; they are inappropriate to genets in which early ramets cease to exist as they produce later ramets. Natural selection cannot operate on what no longer exists.

The only other candidate for a lineage is the ecological community. Boucot (3) does not argue that communities are selected (in either sense of this term), only that they evolve by means of the replacement of one closely

related species by another. May (31) disagrees. The coevolution of species within an ecosystem may give rise to all sorts of interesting patterns, but "ecological systems as such do not evolve." Once again, the problem seems to be the independence of the separate lineages contained within ecological communities. In connection with "arms races" both between and within species, Dawkins & Krebs (8) remark that "it is important to realize who are the parties that are 'racing' against one another. They are not individuals but lineages." Species can interact, but they are not forced to share their "battle plans" the way organisms in the same species must. "In an interspecific arms race like that between predator and prey, two entirely separate lineages coevolve in parallel, mutually countering one another's adaptations, but in the intraspecific arms race the 'lineages' which are racing against each other are not really lineages at all. The genes that programme the development of queen behaviour are present in workers, and the genes that programme the development of worker behaviour are present in the queens."

In sum, genes, organisms, and colonies form lineages. The separate sexes, castes, etc within single species do not. If ecological systems evolve, two different sorts of lineages must be distinguished: those in which the constituent lineages form networks and those composed of independent sub-lineages.

The Prevalence of Sex

The prevalence of sex remains the major roadblock to an entirely "individualistic" interpretation of evolution. As Maynard Smith (33) remarks, "there is however one property, that of sexual reproduction, which is almost universal, and for which the generally accepted explanation involves, implicitly or explicitly, a process of group selection" (see also 32). Williams (57) agrees, noting that "if group selection can produce the machinery of sexual reproduction, it ought to be able to do many other things as well." In a more recent work, Williams (58) sets out several possible individualistic explanations for the prevalence of sex. Each might apply in special circumstances, but none of these explanations taken severally or conjointly, is adequate to explain why the vast majority of species reproduce sexually. In what appears to be near desperation, Williams (58) appeals to "historical constraints that preserve sexual reproduction when it has ceased to be adaptive." In higher vertebrates sexuality is a "maladaptive feature, dating from a piscine or even prochordate ancestor, for which they lack the preadaptations for ridding themselves."

Stanley (45) suggests an even more innovative explanation for the prevalence of sex. According to his species selectionist view, sexual species "predominate simply because they maintain a high capacity for speciation, while

asexual clones do not." Because "almost every species is ephemeral in geologic time," the "impact of extinction upon higher organisms is simply too great to be offset by clonal rates of diversification." Thus Stanley (45) suggests that the "evaluation of sex be elevated to the level of the higher taxon. It is not primarily the species that benefits, but the clade. In effect, sexuality represents a *sine qua non* for success in species selection."

As original—even bizarre—as Williams' and Stanley's explanations are, I do not think they go far enough; they remain imbued with the common-sense notions of genes, organisms, and species. The very statement of the problem assumes that sexual and asexual organisms form comparable "species." For example, Stanley cites White's (52) estimate that about one in a thousand animal species is asexual; but if we take him at his word and agree that asexual organisms neither form species nor are capable of speciating, then clones and species are not comparable. As Stanley (45) himself remarks, his view might better be called lineage selection. What counts in evolution is the level at which lineages form constantly diverging trees. This occurs at the level of single organisms in asexual reproduction and single species in sexual reproduction. If like is to be compared to like, asexual lineages should be compared to sexual lineages, and in such a comparison, sexual reproduction becomes as rare as it should be. The existence of sexual reproduction still must be explained, but the scope of the problem is greatly reduced, so reduced that one or more of the explanations suggested for it might be adequate.

Conclusion

In the introduction to a symposium on sociocultural evolution, Buckley (4) complains that, while most "anthropologists and sociologists today recognize sociocultural systems as group entities at their own ontological stage of organization with emergent features, . . . most biologists have not been able to recognize any level beyond the individual organism in other than aggregative statistical terms (populations, communities, ecosystems)." If the discussion in this paper has done nothing else, it should show that Buckley is mistaken. The following quotation from Maynard Smith (34) should make another conclusion equally apparent—i.e. that understanding evolution seems to necessitate the abandonment of common sense: "Fluctuations may bring a species to extinction in a system. I can accept a moderate amount of this but not very much. Obviously, extinction is more frequent in smaller systems. At a ridiculous extreme every death or every movement creates extinction at that exact point. Robins become extinct in an apple tree many times each day whenever they fly elsewhere. To me, frequent extinction is a signal that the system under study is not large enough to include the processes being studied. Move the system boundaries

out until extinction becomes rare. This ensures that the organizing forces of the system lie within the system, and also solves the problem of frequent extinction."

The reader may now be tempted to agree with Hamilton (20) that "common usage" is preferable to all these "metaphysical" ruminations. As understandable as this temptation is, I suspect that sooner or later common usage will have to be sacrificed if we are to understand the evolutionary process.

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