

## Reviving the Superorganism

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Individuals become functionally organized to survive and reproduce in their environments by the process of natural selection. The question of whether larger units such as groups and communities can possess similar properties of functional organization, and therefore be regarded as "superorganisms", has a long history in biological thought. Modern evolutionary biology has rejected the concept of superorganisms, explaining virtually all adaptations at the individual or gene level. We criticize the modern literature on three counts. First, individual selection in its strong form is founded on a logical contradiction, in which genes-in-individuals are treated differently than individuals-in-groups or species-in-communities. Imposing consistency clearly shows that groups and communities can be organisms in the same sense that individuals are. Furthermore, superorganisms are more than just a theoretical possibility and actually exist in nature. Second, the view that genes are the "ultimate" unit of selection is irrelevant to the question of functional organization. Third, modern evolutionary biology includes numerous conceptual frameworks for analyzing evolution in structured populations. These frameworks should be regarded as different ways of analyzing a common process which, to be correct, must converge on the same conclusions. Unfortunately, evolutionists frequently regard them as competing theories that invoke different mechanisms, such that if one is "right" the others must be "wrong". The problem of multiple frameworks is aggravated by the fact that major terms, such as "units of selection", are defined differently within each framework, yet many evolutionists who use one framework to argue against another assume shared meanings. We suggest that focusing on the concept of *organism* will help dispell this fog of semantic confusion, allowing all frameworks to converge on the same conclusions regarding units of functional organization.

### Introduction

The idea that single-species groups, multi-species communities, and human societies can possess the properties of single organisms is a frequently recurring theme in human thought. Within biology, social insect colonies have been regarded in this fashion for centuries. More recently, Clements (1916) compared the succession of plant species that culminates in a forest, to the growth and development of a single organism. Odum (1969) compared ecosystem processes such as nutrient cycling to the physiological processes of individuals. Wynne-Edwards (1962, 1986) proposes that populations evolve to avoid extinction, just as individuals evolve to avoid their own deaths. Margulis (1970, 1981) proposes that eucaryotic cells are in fact tightly integrated communities of bacteria. Lovelock (1979) even portrays the entire earth as a kind of organism that regulates its atmosphere to be conductive for life.

These theories have a certain magnetic appeal, as their sheer number and popularity among lay-people attests. Nevertheless, the superorganism concept has not fared well within evolutionary biology, which is the one discipline best qualified to judge it. Many evolutionists subscribe to a concept known as individual selection, which holds that groups, communities and human societies are only collections of organisms without themselves having the properties of organisms. Individual selectionists not only regard the existence of superorganisms as a dead issue, but they also regard its death as one of their greatest achievements (Williams, 1966; Ghiselin, 1974; Dawkins 1976, 1982; Maynard Smith, 1987*a,b*). The demise of the superorganism is perhaps best illustrated by the following quotes from modern social insect biologists.

"Despite the logical force of arguments against group (or colony) selection, and the invention of tidy explanations for collaboration in individual terms, the supraorganism (colony-level selection) still haunts evolutionary discussions of insect sociality." (West-Eberhard, 1978, p. 12)

"I know of no observation on honeybee biology which unequivocally demonstrates the action of colony-level selection working at the expense of individual interests." (Seeley, 1985, p. 7)

Thus, according to these authors, even something as organism-like as a bee colony must be understood in individualistic terms.

It is true that many superorganism theories are best regarded as poetic metaphors in scientific guise. To regard the earth's atmosphere as a fragile goddess that needs protection is far more compelling than to regard it as a complex system of gases that needs management. Unfortunately, the metaphor creates an illusion of functional organization where none exists, and presents a misleading image of nature as inherently benign and cooperative. The superorganism concept fails as a grandiose theory of nature, and its death in this form is indeed a triumph of modern evolutionary biology.

Against this background, reviving the superorganism concept might seem like bringing back Dr Frankenstein's well-intentioned monster. Nevertheless, at least five compelling reasons exist for constructing a clearly formulated scientific theory of superorganisms.

(i) Individual selection in its strong form is founded on a logical contradiction. Imposing consistency clearly shows that collections of individuals can become functionally organized by natural selection, in exactly the same way that individuals themselves become functionally organized.

(ii) Conditions for the evolution of superorganisms are not overly restrictive. Superorganisms are more than just a theoretical possibility; they actually exist in nature.

(iii) The theory predicts that only some groups and communities qualify as superorganisms. Others are mere collections of individuals or complex mixtures of adaptation at more than one level. Thus, a legitimate theory of superorganisms is not grandiose, and can avoid the excesses of the past.

(iv) The strong form of individual selection itself is a metaphor that creates a misleading picture of nature as inherently exploitative and competitive. The notion

that all evolved adaptations are brands of self-interest must be substantially modified if individuals sometimes function as "alleles" in group and community "organisms". A legitimate theory of superorganisms might therefore help correct certain excesses of the present.

(v) Major terms surrounding this subject, such as "individual selection", "group selection", etc. have acquired multiple and conflicting meanings. Several conceptual frameworks exist that masquerade as competing theories, but which actually are alternative ways of analyzing a common process of evolution in structured populations. To be correct, each framework must therefore reach the same conclusion about units of functional organization. This convergence can be facilitated by focusing on the concept of organism within each framework.

### Semantics

The term "individual" and "organism" have a variety of meanings in evolutionary biology, and before proceeding it is important to clarify our own usage. Hull (1980) defines individuals as "spatio-temporally localized entities that have reasonably sharp beginnings and endings in time". Notice that this definition makes no reference to functional organization; an atom, a gene, a single creature (such as an insect) and an entire species all are examples of individuals. By contrast, an organism can be defined as "a form of life composed of mutually dependent parts that maintain various vital processes" (Random House dictionary, unabridged edition). Thus, the hallmark of an organism is functional organization. An atom is not an organism, genes (and the organs they code for) are only parts of an organism, and species are frequently only collections of organisms. Because single creatures are, in most respects, both individuals and organisms, biologists informally use the two words interchangeably. The term "individual selection", for example, refers to single creatures, and not to the idea encompassed by Hull's broader definition. We will abide by the colloquial synonymy and refer to single creatures as both individuals and organisms. When more formal definitions are required, we will be careful to identify them as such.

We define a superorganism as a collection of single creatures that together possess the functional organization implicit in the formal definition of organism. Just as genes and organs do not qualify as organisms, the single creatures that make up a superorganism also may not qualify as organisms in the formal sense of the word. We will continue to refer to them as individual organisms, however, to conform to colloquial usage.

### Individuals as Organisms, and the Concept of Heritability

Individuals acquire the exquisite functional organization that justifies their status as organisms by the process of natural selection. As Darwin realized, natural selection requires heritable variation. Individuals must differ in their properties, and those differences also must exist to some degree in their offspring. If so, then properties that enhance the relative survival and reproduction of individuals will increase in

frequency from generation to generation. The accumulation of these properties is the functional organization that allows individuals to successfully survive and reproduce in their environments.

Today we know that heritable variation is caused by differences in the genetic composition of individuals. The modern concept of heritability figures importantly in the theory of superorganisms, so it will be useful to review how it is calculated for individuals (Table 1). Consider two alleles ( $A$  and  $a$ ) at a single locus. The  $A$ -allele detoxifies a metabolite in the bloodstream, increasing both the survival and fertility of individuals carrying the  $A$ -allele. To determine the heritability of this trait, we must first calculate a quantity known as the average effect of each allele. Basically, the average effect is the fitness of an allele, averaged over all the individuals in which the allele exists, and normalized with respect to the mean fitness of the population (Falconer, 1981).

Table 1 shows how average effects are calculated, how the breeding values of individuals and the additive component of variance is calculated from the average effects, and how heritability is calculated as the ratio of the additive component to the total phenotypic variance of individuals in the population. Table 1 also shows how the modern concept of heritability preserves the original notion of resemblance between parents and offspring. For our purpose, however, we can ignore the technical details and stress a single fundamental point. For a trait to be heritable—that is, for offspring to resemble parents—the average effects of the alternative alleles must be different from each other. Putting it another way, for evolution by the natural selection of individuals to occur, one allele—averaged over all the individuals in which it occurs—must be more fit than the alternative alleles in the population.

TABLE 1  
*The Calculation of Heritability*

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Consider a randomly mating population with two alleles ( $A$ ,  $a$ ) at a single locus, in frequencies  $p$  and  $(1-p)$ . The fitness of the three genotypes is  $W_{AA}$ ,  $W_{Aa}$ ,  $W_{aa}$ , and the mean fitness of the population is  $\bar{W} = p^2 W_{AA} + 2p(1-p) W_{Aa} + (1-p)^2 W_{aa}$ .

To calculate the heritability of fitness, we first calculate the average effect of each allele ( $\alpha_A$ ,  $\alpha_a$ ; Falconer, 1981). Consider a number of  $A$  gametes that unite at random with other gametes in the population to form  $p$   $AA$  homozygotes and  $(1-p)$   $Aa$  heterozygotes. The average fitness of these individuals, minus the mean fitness of the population, is the average effect of the  $A$ -allele.

$$\alpha_A = pW_{AA} + (1-p)W_{Aa} - \bar{W}$$

$$\alpha_a = pW_{Aa} + (1-p)W_{aa} - \bar{W}.$$

Next we calculate a breeding value ( $B$ ) for each genotype, which is the sum of the average effects of its gametes:  $B_{AA} = 2\alpha_A$ ,  $B_{Aa} = \alpha_A + \alpha_a$ ,  $B_{aa} = 2\alpha_a$ . The breeding value of an individual is simply the expected fitness of its progeny, expressed as a deviation from the mean fitness of the population.

The variance in breeding values for all individuals in the population is the additive component of variance ( $V_A$ ) and heritability is the ratio of  $V_A/V_P$ , where  $V_P$  is the total phenotypic variance for the trait. Notice that if  $\alpha_A = \alpha_a$ , then all breeding values are the same,  $V_A = 0$  and heritability is zero. By definition there is no correlation between the fitness of parents and the fitness of their offspring, because the progeny of all genotypes have the same expected fitness. Thus, heritability requires one allele to be more fit than others, averaged across all individuals that the alleles occur within.

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### Groups as Organisms, and a Logical Contradiction

Individuals can be regarded as groups of genes that have become functionally organized by natural selection to perpetuate themselves. We can use this analogy to show how groups of individuals can be similarly functionally organized, in which case the individuals acquire the status of alleles and the groups acquire the status of superorganisms.

To see this, imagine the following hypothetical example. An asexual species of insect lays its eggs in pools of stagnant water, within which the larvae develop. Each pool receives exactly  $N$  larvae. Two types of individual ( $A$  and  $a$ ) exist within this population. The  $A$ -type detoxifies harmful chemicals in the water, which increases the survival and eventual reproduction of all larvae growing in the pool. The number of insects emerging from the pool plus their combined offspring is therefore an increasing function of the number of  $A$ -types in the pool. The property of detoxification carries no energetic cost for the  $A$ -types, which survive and reproduce exactly as well as  $a$ -types in the same pool (this assumption will be relaxed below).

Now assume that  $N = 2$  and that eggs are distributed randomly into the stagnant pools. In this case the population structure of individuals within pools is identical in every way to alleles existing within the bodies of diploid individuals. Just as the  $A$ -allele in the preceding example alters the milieu (external to it) of the bloodstream, so also does the  $A$ -type alter the external milieu of the stagnant water. Just as we calculated the heritability of individuals based on the average effects of alleles, so also can we calculate the heritability of groups based on the average effects of member individuals. If the average effect of the  $A$ -type is positive, it is favored by natural selection as surely as is the  $A$ -allele in the preceding example. Just as the  $A$ -allele evolved by individual selection, the  $A$ -type evolves by "group selection". Just as the blood of the organism takes on properties that insure the survival and reproduction of the individual, so also does the water take on a functional organization that insures the survival and reproduction of the group. In addition to detoxification we might even expect other adaptive properties such as oxygen transport and a pathogen defense system. In short, for this model at least, we can consider the individual larvae as alleles in a group "superorganism", literally surrounded by a body of water with the adaptive properties that we normally associate with blood.

Many species of insects inhabit stagnant pools of water, and it would be interesting to determine if they alter the chemical composition of their environment along the lines suggested above (Allee, 1931; 1938). Even if they do, however, many evolutionists would not regard such groups as superorganisms. They would interpret the adaptations at the individual level, because individual larvae that alter their aquatic environment leave more offspring than larvae that do not. The fact that they cause other larvae in their pool to leave more offspring also is regarded as irrelevant, because these larvae are just a random sample from the population and any effect on them, positive or negative, cannot alter global allele frequency change (Nunney, 1985a; Dawkins, 1976, 1979; Maynard Smith, 1987a,b).

This statement is correct, but its use as an argument in favor of individual selection and against group selection involves a logical contradiction. As we have seen,

individuals can be regarded as groups of alleles. When the *A*-allele is more fit than its alternative, averaged over all the individuals within which the alleles occur, this is not regarded as an argument against individual selection. On the contrary, such differences are required for traits to be heritable, and form the very foundation of Darwin's theory. How then can the greater fitness of *A*-individuals, averaged over all groups within which the individuals occur, be used as an argument *against* group selection?

This contradiction is extremely basic, but nevertheless pervades modern evolutionary thought. In our opinion, only two ways exist to impose consistency. The first, which may be termed levels-of-selection theory, is to apply the same standards for genic, individual, group, and community-level selection (Arnold & Fristrup, 1982; Lewontin, 1970; Sober, 1984; Wade, 1978a; Wilson, 1975, 1980, 1983). Within this framework, natural selection can be distributed over a variety of levels and superorganisms become a legitimate possibility. The second way to impose consistency is to use the same argument that denies group-level selection to deny individual-level selection, describing all evolutionary change in terms of the average effects of alleles. This is the approach of Williams (1966, 1986) and Dawkins (1976, 1982), which has become popularly known as selfish gene theory. As Dawkins states, "the fundamental unit of selection, and therefore of self-interest, is not the species, nor the group, nor even, strictly speaking, the individual. It is the gene, the unit of heredity".

We will take the first route to consistency, and then will return briefly to construct a parallel argument within selfish gene theory.

### Conflicts Between Levels of Selection

The model outlined above can be generalized as follows:

- (i) A population is subdivided into a number of groups (see Uyenoyama & Feldman, 1980; Wilson, 1983; and Sober, 1984, for the technical definition of groups).
- (ii) Groups vary in properties that affect the number of dispersing progeny (group fitness).
- (iii) Variation in group fitness is caused by underlying genetic variation that is heritable, i.e. the average effects of the elements composing the groups (alleles and individuals) are not all equal to each other.
- (iv) No differences exist in the fitness of individuals within groups.

When these conditions are met, natural selection endows groups with the same properties of functional organization that we normally associate with individual organisms. Individuals can properly be viewed as genes/organs within a superorganism, and this interpretation is consistent with the fact that some types of individuals are more fit than others, averaged across all groups.

Superorganisms therefore are fully compatible with modern evolutionary theory. It can be argued, however, that the conditions are so unrealistic that superorganisms do not exist in nature. Many populations are not structured into groups [condition (i)], and when they are the groups are sometimes so large that negligible genetic variation exists between them [condition (iii)]. By far the most fragile assumption, however, involves the lack of differences in the survival and reproduction of individuals within groups [condition (iv)]. Returning to the aquatic insect example,

if we assume that detoxifying the water is energetically costly, then *A*-types will have fewer offspring than *a*-types from the same group. The trait is disfavored by natural selection operating within groups, at the same time it is favored by natural selection operating between groups. We therefore have a conflict between levels of selection, and the outcome depends on their relative strengths. Notice that if within-group selection "wins", then the water simply remains polluted water and does not take on the functionally analogous properties of blood.

We can generalize from this example as follows: natural selection can act both within a unit (favoring some elements of the unit over others) and between units (favoring some units over others). When within-unit selection overwhelms between-unit selection, the unit becomes a collection or organisms without itself having the properties of an organism, in the formal sense of the word. When between-unit selection overwhelms within-unit selection, the unit itself becomes an organism in the formal sense of the word.

This framework, which equates "individual selection" with "within-group selection", avoids the logical contradiction mentioned above. In our opinion it has several important implications. First, it prevents the concept of superorganisms from being overly grandiose. Not all groups and communities are superorganisms, but only those that meet the specified (and often stringent) conditions. Second, it prevents the concept of individual selection from being overly grandiose. Not all adaptations evolve at the individual level; a trait does not count as an individual adaptation just because those possessing it are, on average, fitter than those that do not. Third, conflicts between levels of selection do not always result in one level "winning" and another "losing". Sometimes the results is a "compromise", and the unit must be regarded as partially a collection of organisms and partially a superorganism in its own right.

Sex ratio evolution provides a superb example of conflicts among three levels of selection; the gene, the individual, and the group. For groups with an abundance of resources that persist for several generations, between-group selection by itself favors a highly female-biased sex ratio, which maximizes the productivity of the group (Williams, 1966; Colwell, 1981; Wilson & Colwell, 1981; Charnov, 1982; Frank, 1983, 1986). Within-group selection, however, favors an equal investment in sons and daughters, which maximizes the fitness of parents relative to others in the same group (Fisher, 1958; Williams, 1966). The sex ratio that actually evolves depends on the relative strengths of the two opposing levels of selection. Many species that are sub-divided into small multigenerational groups possess moderately female biased sex ratios, signifying that both within- and between-group selection have figured in the evolution of the trait (Aviles 1986; Charnov, 1982; Frank, 1983; Hamilton, 1967; Wilson & Colwell, 1981). At least as far as sex ratio is concerned, these groups are intermediate between superorganisms and mere collections of organisms. Attempts to explain the entire pattern as the maximization of individual fitness, "without invoking group selection" (e.g., Grafen, 1984; Nunney, 1985b; Maynard Smith, 1987a,b), uniformly fall prey to the logical contradiction outlined above, by employing a definition of individual selection that averages the fitness of individuals across groups.

Within-individual selection—the differential reproduction of genetic elements within single individuals—normally is suppressed by the rules of meiosis, which insure that the alleles on diploid chromosomes are equally represented in sperm and eggs. The rules of meiosis sometimes are broken, however, and in any case do not apply to genetic elements located in the cytoplasm (Cosmides & Tooby, 1981). Two such elements that affect sex ratio have been studied in a tiny parasitic wasp (Pteromalidae, *Nasonia vitripennis*). The first resides in the cytoplasm and is transmitted only through eggs, not sperm. Females bearing this element produce all daughters, which is adaptive for the cytoplasmic element but not for the chromosomal DNA in the same wasp (Skinner, 1982).

The second element is transmitted only through sperm, but is not a part of the chromosomal DNA. Wasps have a haplo-diploid genetic system in which daughters and sons develop from fertilized and unfertilized eggs, respectively. Consider a male containing this second element that mates with a female. Sons develop from unfertilized eggs, and therefore will not contain the element. Daughters develop from fertilized eggs and will contain the element, but (being females) will not make sperm. How then is the element transmitted? It actually destroys the paternal chromosomes, converting the fertilized egg into a haploid that develops into a male (Werren *et al.*, 1981; Werren *et al.*, 1987). This is the ultimate in conflict between genetic elements within single individuals.

Examples of within-individual selection are fascinating, because they show how much the concept of organism depends on functional organization, and how much functional organization depends on the level at which natural selection operates. The rules of meiosis usually allow between-individual selection to dominate within-individual selection, which endows individuals with the functional organization that we take for granted. In those cases where the rules of meiosis break down, however, it is the genetic elements that acquire the status of purposeful organisms. At least as far as sex ratio is concerned, the wasp is partially a mere collection of quarreling genes, without itself having the functional organization required by the formal definition of organism.

### **The Evolution of Population Structure, and Group-level “Rules of Meiosis”**

Individual organisms are paradigms of functional organization because the rules of meiosis usually suppress within-individual selection, concentrating natural selection at the between-individual level. Following the rules of meiosis is not just something cells happen to do, however, but is itself the product of natural selection (Crow, 1979; Buss, 1987). Thus, a trait that changes population structure, altering the balance between within- and between-individual selection, can itself be favored by natural selection. By extension we might ask if higher level analogs to the rules of meiosis exist that suppress the differential advantage of individuals within groups, thereby concentrating natural selection at the between-group level.

To put the matter concretely: if a population is structured into groups, such that within- and between-group selection both operate, and a mutant trait appears that reduces selection within groups [condition (iv) listed above], increases the variation

among groups [condition (iii)], or in any other way alters the balance between levels of selection, under what conditions will the trait spread through the population?

This question has received surprisingly little attention from evolutionary theorists (Gadgil *et al.*, 1983; see also Getz, 1981; Sherman & Holmes, 1985; Blaustein & Emlen, 1982, in the context of kin recognition). The following conclusions, however, follow directly from levels-of-selection theory. First, if suppressing within-group selection or enhancing between-group selection is the only effect of the trait, it will indeed be favored by natural selection. Second, the trait specifically is favored by between-group selection. It does not spread by increasing in frequency within groups, but rather by increasing the productivity of the groups that contain it, relative to other groups. Third, if the trait has two effects (pleiotropy), one that alters population structure in favor of between-group selection and another that causes the trait to decline in frequency within groups, it may not spread through the population. In this respect it does not differ from any other trait subject to opposing levels of between- and within-group selection.

The fact that between-group selection favors modifications of population structure that further enhance between-group selection suggests a positive feedback loop that might ultimately suppress within-group selection, just as the rules of meiosis suppress within-individual selection. On the other hand, this loop requires a degree of between-group selection to get started, and also the existence of traits that can modify the population structure without being too severely disfavored within groups. It would be futile to speculate beyond this point, but the concept of population structure as a product of natural selection, in addition to being a factor that determines the outcome of natural selection, clearly deserves more thorough study.

### Examples of Superorganisms in Nature

The view that group selection is a trivial force in nature can be attributed largely to the logical contradiction outlined above, which posits a double standard for conceptualizing group and individual selection. Within the framework of levels-of-selection theory, between-group selection is a conceptual necessity and a significant factor in the evolution of many traits, such as female biased sex ratios (reviewed above) and the evolution of avirulence in disease organisms (Lewontin, 1970; Wilson, 1983). Groups within which these traits are expressed should be regarded as intermediate between collections of organisms and superorganisms in their own right. In addition, it appears that natural selection sometimes is sufficiently concentrated at higher levels to produce single-species groups and multi-species communities that approach individual organisms in their degree of functional organization. Three examples will be described briefly.

#### THE SOCIAL INSECTS REVISITED

Colonies of the eusocial ants, bees, wasps and termites have for centuries been paradigm superorganisms. Sterile castes with specialized functions, colony-level thermoregulation and patterns of information processing that transcend single brains all suggest intuitively that the colonies are functionally organized units, built out

of individual insects (Wilson, E. O., 1971, 1985). Early social insect biologists were unanimous in this interpretation (e.g., Wheeler, 1911; Sturtevant, 1938; Emerson, 1960). With the notable exception of E. O. Wilson (1971, 1975, 1985), however, the superorganism concept has been discarded by modern social insect biologists. What happened to produce such a remarkable transformation of views?

One factor was the realization that natural selection can occur within single colonies, evolving behaviors that are genuinely dysfunctional at the colony level (West-Eberhard, 1978, 1981; Wilson, E. O., 1985; Seeley, 1985). For example, the optimum sex ratio can be different for queens and workers (Trivers & Hare, 1976; Oster & Wilson, 1978) in much the same way that it differs for chromosomal and cytoplasmic genetic elements within individual organisms (Cosmides & Tooby, 1981). As outlined above, social insect colonies really do cease to be superorganisms, to the extent that natural selection operates within single colonies.

In addition, however, Hamilton (1964a,b) initiated a pervasive trend towards interpreting colony function itself as a form of individual advantage. Hamilton's inclusive fitness theory weights the effects of an actor on itself and recipients by the genetic similarity between actor and recipients to calculate allele frequency change. By this reasoning, a bee that helps her mother raise offspring can have a higher inclusive fitness than if she attempts to raise offspring herself. Even sterility can be inclusive fitness maximizing for the sterile individual, which for many evolutionists makes between-colony selection appear unnecessary.

There is no question that inclusive fitness theory is an insightful way of looking at natural selection. Hamilton (1975), however, was among the first to realize that it merely is a different way of expressing natural selection operating at multiple levels, and therefore cannot be used as an argument against between-group selection. Putting it another way, maximizing inclusive fitness requires between-group selection. To see this, consider a mutant behavior expressed in sterile workers that increases the fecundity of the queen. The behavior obviously increases the inclusive fitness of the worker, but the frequency of the allele does not increase within the colony. It evolves only by between-colony selection; colonies bearing the allele out-reproduce colonies that do not.

Despite numerous demonstrations that maximizing inclusive fitness requires between-group selection (Hamilton, 1975; Wilson, 1977, 1980; Wade, 1978a, 1980; Uyenoyama & Feldman, 1980; Michod, 1982), West-Eberhard (1981) and Seeley (1985) treat them as separate processes, such that if a behavior can be explained with an inclusive fitness argument, invoking between-colony selection is said to be unnecessary and even misguided. We do not wish to single out these authors, however, because the confusion is epidemic and stretches all the way back to Maynard Smith's (1964) original distinction between group selection and kin selection (Wilson, 1983, 1987; Taylor & Wilson, 1988).

To summarize, evolution in the social insects is dominated by between-colony selection, endowing colonies with the functional organization normally associated with individuals. E. O. Wilson (1985) is fully justified in comparing the "sociogenesis" of insect colonies with the morphogenesis of individual bodies. At the same time, the potential for within-colony selection should not be overlooked.

The widespread modern view that colony-level selection is unnecessary, that no unequivocal evidence for it exists, and that the superorganism concept is obsolete, are all derived from the fallacy that inclusive fitness theory does not require between-colony selection.

#### CELLULAR SLIME MOLDS

About 50 species of "social" amoebae are known that forage as individual cells but then aggregate into a multicellular body (called a slug) that migrates a distance and builds itself into a tower for purposes of dispersal (Bonner, 1982*a,b*). In many species the tower is morphologically differentiated into reproductive spores supported by a non-reproductive stalk. Thus, cellular slime molds are groups that have achieved the ultimate in division of labor matched only by the cells of individual organisms and the castes of eusocial insects.

The functional organization of cellular slime molds seems vulnerable to within-group selection. What prevents the evolution of traits that cause cells to preferentially become spores, thereby reproducing at the expense of stalk-forming cells (Armstrong, 1984)? Such "freeloading" types in fact exist both in nature (Buss, 1982) and the laboratory (Filosa, 1962), but in the few known examples they do not attain a density above 10% in the population.

At least three scenarios can explain the dominance of between-group selection for slime molds. First, consider a number of spores that hatch into solitary amoebae that forage and divide repeatedly until it is time to reaggregate. If the original spores were widely separated from each other, each reaggregation might assemble clonal descendants of a single ancestral spore. If so, genetic differences between slugs would be maximal [condition (iii) outlined above, favoring between-group selection], and within-group selection would have little chance to operate. A trait causing a cell to "refuse" to become a stalk would be concentrated in slugs consisting entirely of such cells, which would form lumps of unelevated spores. Although the microdistribution of cellular slime molds is patchy (Sienberg, 1976; Kuserk, 1980; Buss, 1982), it is extremely unlikely that lineages are spatially isolated to this extent.

The second scenario assumes that spores are not widely separated; their descendants mix during the solitary foraging stage. Nevertheless, descendants still may resegregate into genetically uniform slugs if a recognition system exists to distinguish clone-mates from other cells (Buss, 1982). This scenario is identical to the first, except that between-group selection is maintained by an evolved adaptation (the recognition system), rather than a pre-existing population structure (widely separated spores). Similarly, Armstrong (1984) speculates that restricted movement during the solitary stage might evolve as an adaptation to enhance variation among groups.

The third scenario assumes that single slugs are not genetically uniform, but contain descendants from numerous ancestral spores. Within-group selection is suppressed, however, by traits that prevent cells from biasing their probability of becoming spores [condition (iv) outlined above]. For example, non-genetic differences between cells (such as age) figure importantly in the aggregation and early development of the slug (Bonner, 1982*a*; MacWilliams & Bonner, 1979; McDonald,

1984). Approximately half-way through the 12-hr process, however, a mixing phase occurs that randomizes the position of individual cells in the slugs (Bonner & Adams, 1958). Thereafter the positions become relatively fixed and the front end differentiates into a stalk. A set of traits that first randomizes, and then freezes cell position might act as a group-level "rule of meiosis," giving each cell a relatively equal probability of becoming a spore.

All three scenarios acknowledge that natural selection is concentrated at the between-group level for the dispersal stage of cellular slime molds, but differ in the underlying reasons. The first assumes a pre-existing population structure that favors between-group selection. The second assumes an evolved population structure that enhances genetic variation among groups. The third assumes an evolved population structure that suppresses natural selection within groups. The third scenario also points out a common misconception among evolutionists; that a group may be considered an individual only when it is a genetically uniform clone (Alexander & Borgia, 1978; Williams, 1986a, b). The essential criterion is absence of within-group selection, which may be accomplished either by creating genetically uniform groups, or by suppressing the differential reproduction of genetically diverse groups.

#### PHORETIC ASSOCIATIONS

Our final example of superorganisms is at the level of multi-species communities. Many resources in nature are both patchy and ephemeral; patchy in that they are relatively discrete and widely dispersed, and ephemeral in that once consumed they are not renewed. Examples include carrion, dung, and stressed timber. These resources tend to be exploited by highly specialized insect species that have evolved remarkable abilities to detect them. Even more remarkable, however, are the many species of wingless creatures such as mites, nematodes, fungi and microbes that also have evolved to specialize on patchy ephemeral resources. These creatures solve the problem of dispersal by hitch-hiking on the bodies of the insects, an interaction that is termed phoresy. Thus, when the insects colonize a fresh resource patch, they carry with them an entire multi-species community of phoretic associates, who disembark to pursue a free-living existence. The density and diversity of phoretic communities can reach spectacular proportions. For Silphid beetles in the genus *Nicrophorus* (specialized carrion feeders that reproduce on small carcasses), a single beetle frequently carries over 500 mites of several species, several thousand nematodes and countless microbes. It is one of the wonders of natural history that when a mouse dies in the forest, within hours it becomes the resource for a diverse specialized community that has been evolving for millions of years (Wilson & Knollenberg, 1987).

It is easy to imagine how natural selection might operate at the level of multi-species communities for phoretic associations. Consider a large number of resource patches, each of which develops into a community composed of the insects, their phoretic associates, plus other species that arrive independently. The community of phoretic associates may be expected to vary from patch to patch in species composition and in the genetic composition of the component species. Some of

these variant communities may have the effect of killing the carrier insect. Others may have the effect of promoting insect survival and reproduction, and these will be differentially dispersed to future resource patches. Thus, between-community selection favors phoretic communities that do not harm and perhaps even benefit the insect carrier. At the extreme, we might expect the community to become organized into an elaborate mutualistic network that protects the insect from its natural enemies, gathers its food, and so on. On the other hand, within-community selection may well favor genotypes and species that treat the insect as a resource, compete for its food, or otherwise increase their fecundity at the insect's expense. Once again we have the potential for conflict between levels of selection.

The empirical data suggest that between-community selection often plays a strong role in the organization of phoretic associations. Far from a cargo of parasites and competitors, most phoretic associations that have been studied in detail have a striking absence of negative effects on their carrier, and many have positive effects (reviewed by Wilson & Knollenberg, 1987). In some cases the degree of mutualism reaches the extreme described above, and the carrier insect literally dies if deprived of its phoretic associates who both protect and feed it. For example, beetles of the family Scolytidae tunnel under the bark or within the heartwood of trees, depositing their eggs in specially created niches. The tunnels and niches together are called a gallery. Trees have defences against Scolytid beetles, which usually includes flooding the galleries with resins. Many species of beetle carry a pathogenic fungus (*Ceratocystis minor*) that kills the tree in the vicinity of the gallery, disabling its defenses. A multi-species assemblage of fungi and yeasts that does not include *Ceratocystis* is deposited inside the niche with the egg. This community spreads out into the surrounding plant tissue and grows into a velvety mat around the walls of the niche. The larva feeds entirely from the fungal mat, which not only provides basic nutrients but possibly also specific vitamins lacking in the tree and manufactured by the phoretic associates (Haanstad & Norris, 1985; Kok, 1979). Notice that within-community selection favors unpalatable forms at this stage, but evidently is overwhelmed by between-community selection that causes the more palatable forms to be dispersed to future resource patches. The larva transforms into an adult, takes a final meal, stuffs part of the fungal mat into a special structure called a mycangium, and exits the niche. On its way through the tunnel system it picks up spores of the pathogenic fungus, and also mites that themselves carry spores of the pathogenic fungus in mycangium of their own (Bridges & Moser, 1983). It is not an exaggeration to call such a functionally organized community a multi-species superorganism (Francke-Grossman, 1967; Whitney, 1982).

### A Proposed Experiment

The existence of functionally organized communities in nature suggests that they might also be produced in the laboratory by artificial community-level selection. Consider growing a large number of plants in flower pots and then ranking the plants according to size. In one experiment, seeds from the largest plants are selected to grow in a new set of pots (a standard artificial selection experiment). In a second

experiment, soil from beneath the largest plants is selected and used to inoculate a new set of pots with sterilized soil, in which a new generation of plants is grown.

It is important to emphasize the similarity between these two experiments. Plant size is influenced both by genes on the inside and by the soil community on the outside of the plant. Understanding the genetic determinants of plant size will take many lifetimes, but fortunately we need not wait for such a detailed causal understanding. If the plants vary in their genetic composition in a way that is causally related to yield, then by picking seeds from the largest plants we are selecting a sample of genes that is biased toward producing large plants. The prediction is purely empirical, but effective nonetheless.

In the same way, it will take many lifetimes to understand the numerous effects that soil bacteria, fungus, nematodes, etc. have on plant growth. We still can create a large number of soil communities, however, that vary in their species composition and also the genetic composition of the component species. By picking soil from beneath the largest plants, we might select a sample of soil communities that is biased towards producing large plants. Iterating this procedure many times, we might winnow a refined sub-set of the original spectrum of communities that is functionally organized to increase plant yield, just as phoretic associations can be functionally organized to protect and nourish their insect carriers.

As always, the second experiment will not work if the differential reproduction of species and genotypes within pots overwhelms the between-pot selection that constitutes the experimental procedure. The magnitude of conflict between levels of selection is an empirical question that can only be answered by doing the experiment. Unfortunately, community-level selection has never to our knowledge been attempted in the laboratory, even though the procedure is straightforward and the economic benefits potentially great. It simply never occurred to any biologist that communities could be treated as entities with heritable variation and selected accordingly. Perhaps this says something about the very different ways that individuals and communities are perceived in the minds of biologists.

### The Selfish Gene Framework

We have shown that, within the framework of levels-of-selection theory, natural selection is distributed across a nested hierarchy of units from genes to multi-species communities. We also have provided empirical evidence that higher levels of selection can be strong forces in nature, endowing groups and communities with the functional organization normally associated with individual organisms. As we mentioned earlier, however, another logically consistent framework exists in the form of "selfish-gene theory", which recognizes higher levels of selection as a theoretical possibility, but which denies them importance in nature. How can such different conclusions be reconciled with each other?

Selfish gene theory is based on the observation that individuals, groups, and communities do not persist through evolutionary time, but periodically dissociate into their elements which reform in different combinations. As Williams (1966) put it, Socrates' genotype existed only once in the history of life on earth, and therefore

did not have the persistence required to be a "unit of selection". Only the elements composing the higher units—ultimately the genes—persist long enough to be modified through evolutionary time.

Sober (1984) examines selfish gene theory in detail, but here we need to stress only a single fundamental point: defining the gene as the "ultimate" unit of selection does not alter the fact that individuals are usually organisms, in the formal sense of the word. If individuals are organisms, and they are not termed "units of selection," then within the framework of selfish gene theory the "units-of-selection" concept must be irrelevant to the question of functional organization.

This is yet another example of the semantic confusion that plagues modern evolutionary biology, caused by the co-existence of conceptual frameworks that use the same terms in different ways. Within levels-of-selection theory an entity must be a unit of selection to become functionally organized. Within selfish-gene theory an entity can be functionally organized without being a unit of selection. Yet these two frameworks are routinely pitted against each other as if they are talking about the same thing (Wilson, 1983)!

If we remain within the framework of selfish gene theory, and ask the question "What causes an entity to become an organism?", we find that selfish gene theory must give back exactly what it took away—a nested hierarchy of units which it calls "vehicles of selection" rather than "units of selection". Thus, individuals are organisms because they are vehicles of selection, and if individuals can be vehicles then groups and communities can be as well.

Dawkins (1982, p. 114) appears to recognize this, but then makes the empirical claim that individuals usually are vehicles of selection, while groups and communities almost invariably are not. He even compares the search for higher vehicles of selection to the futile search for a perpetual motion machine. We suggest that Dawkins' empirical claim is demonstrably false. The "vehicle" concept in selfish-gene theory is identical with the "unit" concept in levels-of-selection theory, and all the evidence reviewed above for higher units applies equally to higher vehicles. Even selfish gene theory must conclude that functional organization is distributed among a hierarchy of units, and that superorganisms exist in nature.

### Avoiding the Excesses of the Past

The notion that people act for the good of their group or their larger society is a dominant theme in everyday life. The scientific idea that non-human creatures evolve to benefit their groups and communities probably originated as an expression of the same sentiment. During the last two decades, evolutionists have shown that it fails as a grandiose theory of nature. Traits frequently evolve that benefit some individuals at the expense of others, with dire consequences at higher levels. This is a hard-won insight that must be retaught to every generation of students who import the original sentiment from their everyday lives.

Nevertheless, we have demonstrated that superorganisms are fully compatible with modern evolutionary theory, that they exist in nature, and might even be artificially selected in the laboratory. Some evolutionists are alarmed at the prospects

of legitimizing superorganisms to this extent. Commenting on Sober's (1984, 1987) treatment of levels-of-selection theory, Maynard Smith (1987b) even implies that the progress of decades will be destroyed, plunging evolutionary biology back into a dark age:

"It is therefore perfectly justified to study eyes (or, for that matter, ribosomes, or foraging behaviors) on the assumption that these organs adapt organisms for survival and reproduction. But it would not be justified to study the fighting behavior of spiders on the assumption that this behavior evolved because it ensures the survival of the species, or to study the behavior of earthworms on the assumption that it evolved because it improves the efficiency of the ecosystem . . . This point may seem so obvious as not to need stressing. I can only say that it was not obvious to everyone twenty years ago. If Sober's way of describing the world is taken seriously, it will again cease to be obvious, and someone (not me, next time) will have the job to do over again." (pp. 147-148).

Time will tell whether a theory of superorganisms creates a rash of uncritical thinking. The theory itself, however, is not grandiose and predicts where superorganisms do not exist as clearly as where they do. The earth's atmosphere may be heavily influenced by life on earth, but life on earth is most unlikely to be a single organism that has evolved to regulate its atmosphere (Lovelock, 1979; Margulis, 1981). Natural selection at any level requires a population of units, and there is only one earth. Yet when the "planet" is the life in a pool of stagnant water, adaptive control of the "atmosphere" becomes more plausible. The artificial selection experiment described above might produce pathways of energy flow and nutrient cycles that are designed, by between-pot selection, to increase plant growth. It even is possible that mutualistic soil communities have evolved by a similar process in nature. But functional design cannot be attributed to ecosystems in general (Odum, 1969). Social interactions may sometimes evolve as group-level adaptations, increasing the fitness of some groups relative to others, but the sweeping interpretation of most social interactions in this fashion (e.g., Wynne-Edwards, 1962, 1986) is doomed to failure. Grandiose superorganism theories can be most effectively refuted by insisting on evolutionary mechanisms. Flat assertions that superorganisms lie outside of Darwinian theory (Maynard Smith, 1987*a,b*), or require such implausible conditions that they never exist in nature (Dawkins, 1982), are quite unnecessary.

### Avoiding the Excesses of the Present

In one sense, levels-of-selection theory is a radical departure from the individualistic theories that have dominated evolutionary biology for the last twenty years. Most evolutionists have been taught, and many still teach their students, that higher levels of selection are so unlikely that they can safely be ignored. As a result, virtually all adaptations are explained in terms of benefits to individuals (or genes), and consequences for groups and communities are considered irrelevant. At the extreme, the entire process of natural selection is characterized by a metaphor of selfishness embodied in the concept of "selfish genes".

Nevertheless, virtually all evolutionists accept a notion of unselfishness that is implicit in the relationship between an organism and its parts. As Maynard Smith

himself states in the passage quoted above, it is justified to study genes and organs on the assumption that they evolved to benefit the organism. For within-group/between-individual selection, it is literally correct to say that alleles evolve when they increase the relative fitness of the individuals possessing them. Levels-of-selection theory shows that the “unselfish” relationship between genes in individuals can legitimately be extended to individuals in groups and species in communities. Contrary to Maynard Smith’s statement, it can be justified to study the behavior of individuals on the assumption that it evolved to benefit a group, or the properties of species on the assumption that they evolved to benefit a community—*to the extent that between-unit selection dominates within-unit selection*. A theory that establishes groups and communities as functionally organized entities in their own right invalidates the metaphor of selfishness as a grandiose principle of nature.

### On the Co-existence of Conceptual Frameworks in Evolutionary Biology

Evolutionary biology is both blessed and cursed with a multitude of conceptual frameworks for analyzing evolution in structured populations. It is blessed because any single framework provides limited insight, and can be insensitive to other insights that appear obvious within other frameworks. No one denies that selfish gene theory and other approaches that average the fitness of individuals across groups have reaped a harvest of insights about the evolutionary process. On the other hand, it is odd that the evolution of population structure is a virtually unexplored subject, that the artificial selection of communities has never been attempted, and that phoretic associations are studied primarily because of their status as economic pests. These subjects, basic and important within the framework of levels-of-selection theory, have somehow been invisible to gene- and individual-selectionists.

A diversity of frameworks also is a curse, however, because by carving up the same subject in different ways these frameworks inevitably create polymorphisms in the meaning of words such as “altruism”, “selfishness”, “group selection”, “individual selection” and so on. One might hope that evolutionists could develop a different terminology for each framework, or at least be careful to specify the set of definitions they are using, but historically this has not been the case. Even the inventors of new frameworks often are unaware that their “new theory” is really just a different way of carving up the old subject. Inclusive fitness theory, selfish gene theory, and evolutionary game theory were all developed in part as “alternatives” to the process of group selection, without any explicit recognition that between-group selection is firmly embedded in their own structures. As a result, evolutionists tend to treat alternative frameworks as competing theories that invoke different processes, such that if one is “right” the others must be “wrong”. It would be hard to overestimate the amount of wasted effort that has been thrown into this endeavor. The statement “eusociality evolved by kin selection” cannot be pitted against the statement “eusociality evolved by between-colony selection”. The statement “phoretic associations are mutualistic because of between-community selection” cannot be pitted against the statement “phoretic associations are mutualistic because genes in associates that increase the fitness of the carrier are more fit than

neutral or detrimental genes". All of these statements are correct, and mere recognition of their compatibility would be an important advance for evolutionary biology.

Alternative conceptual frameworks do compete with each other, but in a different way than alternative hypotheses that invoke different causal mechanisms. A hypothesis that fails is discarded in favor of one that succeeds. If two conceptual frameworks appear to make different predictions, the one that fails can usually be shown in retrospect to "really" predict the successful result. Thus, selfish gene theory "really" predicts the existence of superorganisms, despite the appearances of the last two decades. In this fashion, alternative conceptual frameworks are like competing sports teams; they win or lose on specific issues, but nevertheless persist to meet again. This is a healthy process, but only if it can be distinguished from the testing of alternative hypotheses that really are mutually exclusive. Perhaps in the future we can look forward to a more harmonious co-existence of conceptual frameworks, and a widespread understanding of the relationships between them. Only then can all frameworks converge on a common awareness that the properties of *organism* are not restricted to single creatures, much less to genes, but rather can be distributed over a hierarchy of units from genetic elements within single creatures to multi-species communities.

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