

ORGANISMS, INDIVIDUALS, AND UNITS OF
SELECTION

I. WHY ORGANISMS?

We often think of science—and of philosophy as well—as a process by which puzzlement is removed. This suggests that progress in a science is to be measured by the degree to which it eliminates problems rather than creating them. We sometimes say of an idea that “it raises more problems than it solves.” The fact that this remark is used to state a criticism perhaps indicates that we think of problems as if they were rashes on the skin of the body scientific. Scientific progress makes rashes go away.

However much we may accept this image of science, we must not neglect a reciprocal aspect of scientific change. The creation of problems—the discovery that some fact needs to be explained, where earlier it was accepted as obvious and commonsensical—is fundamental to the scientific enterprise. In fact, it is arguable that major scientific breakthroughs often involve the discovery of new problems, as well as the formulation of solutions. A new way of posing a question is often the prelude to a new answer.

One of the most basic facts about our everyday understanding of the living world is that it is populated by organisms. Organisms are functionally integrated entities; they have parts of different sorts and these parts interact so as to sustain the organism and allow it to reproduce. The idea is so familiar that it is easy to miss the fact that it is really very puzzling. It is the nature of this puzzle and the biological framework for solving it that I want to discuss.

The idea that the complexity and adaptedness of organisms requires explanation is as old as the sun. Long before Darwin, philosophers and theologians recognized that this observation needs to be explained. The design argument for the existence of God was introduced to fill the void. Organisms exist and have the characteristics they do because God—an intelligent designer—made them that way. Darwin focused on the same phenomenon, but substituted a naturalistic for a theological explanation.

The question I am trying to isolate is *not* the one that asks: “Why are organisms *adapted*?” Rather, I want to focus on the query: “Why are *organisms* adapted?” What’s the difference between these two queries? The first asks why organisms are adapted rather than not adapted. The second asks why it is

organisms, rather than objects at some other level of organization, that are adapted. These questions are as different as the two that ask "Why are we having bagels *for dinner*?" and "Why are we having *bagels* for dinner?"

When I ask why it is organisms, rather than other biological objects, that are adapted, this question may sound like it has a false presupposition. Are not species well suited to their continued survival? Cannot the same be said for multi-species communities? And aren't genes, cells, and organs functionally integrated as well? Naively, it may seem that all of nature—nature at every level of organization—is well-adapted.

It cannot be overemphasized that evolutionary theory has rejected the idea that nature is adapted to the ends of survival and reproduction for objects at all levels of organization. R.A. Fisher [1] puts the point succinctly:

It will be observed that the principle of Natural Selection . . . refers only to the variation among individuals (or co-operative communities), and to the progressive modification of structure or function only in so far as variations in these are of advantage to the individual, in respect to his chance of death or reproduction. It thus affords a rational explanation of structures, reactions, and instincts which can be recognized as profitable to their individual possessors. It affords no corresponding explanation for any properties of animals or plants which, without being individually advantageous, are supposed to be of service to the species in which they belong.

This distinction was unknown to the early speculations to which the perfection of adaptive contrivances naturally gave rise. For the interpretation that these were due to the particular intention of the Creator would be equally appropriate whether the profit of the individual or of the species were the objective in view. The phrases and arguments of this pre-Darwinian viewpoint have, however, long outlived the philosophy to which they belong. It would be easy to find among modern writers many parallels to the thought expressed in the following quotation "Of what advantage could it be to any species for the males to struggle for the females and for the females to struggle for the males?"

This sort of question might appropriately be put to an opponent who claimed that the instincts of animals were in each case due to the direct contrivance of the Creator. As a means of progressive change, on the contrary, Natural Selection can only explain these instincts in so far as they are individually beneficial, and leaves entirely open the question as to whether in the aggregate they are a benefit or an injury to the species.

In the paragraph immediately following this passage, Fisher somewhat tempers this picture of natural selection. He says that species-level adaptation, which requires competition among species, is not impossible, but is probably rather unimportant. He then says that the evolution of sexual reproduction might possibly count as an exception to this constrained picture of how natural selection operates.

Fisher had a very definite picture of which level of organization is the level at which adaptations accumulate. Other evolutionists have disagreed with Fisher's conception. My point now is not that Fisher was right or wrong, but

that he recognized that any reasonably precise formulation of the theory of natural selection will have to make decisions about whether it is organisms or species or communities, or some definite combination of the above, that are, as we now say, units of selection. As Fisher remarks, this is a simple, but fundamental, point of advance of evolutionary theory over pre-Darwinian thought about adaptation.

Why can't the theory of natural selection be all things to all levels? That is, why can't it view all adaptations as good for the organism, for the group, and for the community of cohabiting species? The reason is that the interests of these different objects can *conflict*. As Fisher says, a trait of an individual can be good for the species but deleterious for the individual possessing it. If the trait becomes common, then it will be a species-level adaptation, not an individual-level adaptation. If the trait is eliminated, the characteristic that supplants it will be an individual adaptation, but not an adaptation that exists for the good of the species. Because what is good for one level can be bad for another, biologists have had to construct their models of natural selection so that these models allow some kinds of adaptations to evolve, but not others.

Fisher was neither the first nor the last evolutionist to discuss the units of selection problem [2]. Why has the problem lingered so? If models of natural selection make different predictions about what sorts of adaptations will exist in nature, why wasn't the problem of the units of selection quickly settled by a few pertinent observations? The answer to this important question has several parts. Two facts about the power of observation bear mentioning here.

First, it often isn't clear from simple observation what the costs and benefits of a given characteristic are to the various levels of organization one wishes to consider. Fisher mentions the evolution of sexuality. It is true to this day that the evolution of sex is deeply puzzling. There are numerous arguments that show different ways in which sex can be individually advantageous. There also are numerous arguments that show how it can be individually deleterious, though good for the species. There are many models, each of them mathematically correct. It is hard to know which of those models actually bears on the evolution of real organisms. One somewhat daunting possibility is that sex evolved for different reasons in different lineages. If so, there will be no single answer to the question of why sex evolved.

A second reason that it has been hard to settle the question of the units of selection by straightforward observation is that characteristics often have benefits that are unconnected with the reason they evolved. In his book *Adaptation and Natural Selection*, G.C. Williams describes a simple example [3]. Consider a population of deer. These deer are pursued by predators, so it is

to each deer's advantage to be able to run faster rather than slower. Let us consider this population at three stages. Initially, all the deer are slow. Then a mutant or migrant fast deer appears. Finally, after selection has run its course, all the deer in the population are fast.

Imagine that we come on this population at the end of the process. We see that all the deer are fast. We do not see the historical process that has produced this result. How are we to explain what we see?

One possibility is to say that there has been individual selection for being fast. This casts the organism as the unit of selection. Another possibility is that we might say that herds of fast deer are less likely to go extinct than herds of slow deer. In this case, we would say that the speed of the herd is a group adaptation.

The problem of the units of selection is an *historical* problem. It isn't enough to say that the trait we observe is *presently* good for the individuals or for group. The relevant question is *why* the trait evolved. This involves figuring out what the costs and benefits were *in the past*. The difficulty is that the present state of the population is not always a crystal-clear guide to what happened historically.

If selection occurred in the context of a single population, with fast deer outsurviving and outreproducing slow ones, then speed is an individual-level adaptation. If selection occurred among an ensemble of populations, with fast herds outsurviving and reproducing slow ones, then the trait might be a group-level adaptation. However, if each of these hypothetical processes would have reached the same end state, it will be impossible to infer which process actually occurred by observing the end state. The evolutionary process, in this case, will have been *information destroying* [4].

Williams uses the contrast between *group adaptation* and *fortuitous group benefit* to make this point. The problem of the units of selection is not settled by going to nature and seeing whether presently existing characteristics benefit the groups in which they occur. A present benefit may be either a group adaptation or a fortuitous group benefit. Indeed, the same ambiguity attaches to questions about other levels of organization. A trait that now benefits organisms may or may not have evolved by a process of organismic selection.

When we observe the group, we see that it is composed entirely of deer whose top running speed is a certain number of miles per hour. To figure out why this trait evolved, we need to know which other traits were present historically. But these alternatives are not something we observe in the present. Natural selection has destroyed the variation on which it operated. Unfortunately, this means that the process has destroyed some of the evidence

that would help us figure out how the process proceeded. This general feature about natural selection has helped make the units of selection problem a difficult one to resolve.

The problem, however, has not been limited to the difficulty of mustering telling observations. There also has been a conceptual component—of knowing how to think about multi-level selection processes in an appropriate way. In what follows, I'll try to clarify some of the key concepts involved in this biological problem. This clarification will involve identifying some red herrings. The relative frequency of red herrings among the arguments that have grown up around this problem suggests that the units of selection problem requires conceptual clarification before it can be settled empirically.

II. ALTRUISM

Historically, the problem of the units of selection was centered on the question of whether organisms have characteristics that are good for the group though deleterious for the organisms possessing them. Biologists have used the term "altruism" to label such traits. The biological term has been stripped of the mental content that it possesses in ordinary language. To say that a plant behaves altruistically when it leeches a pesticide into the soil does not involve attributing a mind or motives to the plant. It merely means that the plant helps other plants at some cost to itself. Help and hurt are calculated in the currency of fitness—of effects on survival and reproduction [5].

An altruistic characteristic, thus defined, cannot evolve by natural selection, if selection occurs within the confines of a single population. If some individuals donate fitness benefits to others, whereas others receive those benefits but fail to reciprocate, the donors will be less fit than the free riders. As a result, the "selfish" characteristic of being a free rider will increase in frequency and altruism will decline. In the limit, altruism will be eliminated by the competition between organisms within the population.

On the other hand, if groups compete against other groups, then groups of altruists may do better than groups of selfish individuals. The success of altruistic groups over selfish ones may be sufficient to offset the fact that within each group, selfish individuals do better than altruists. The result may be that altruism evolves and is maintained in the ensemble of populations. I'll discuss in a moment how this is possible.

Altruism is not only interesting in its own right. It is, in addition, a useful characteristic to look for, if one wishes to know whether the adaptations found in nature exist for the good of the organism or for the good of the group. If

adaptation is solely for the good of the organism, then there should be no altruism. On the other hand, if adaptations are sometimes for the good of the group, then one might hope to establish this by finding genuine altruism in nature. Contrary conceptions of adaptation make contrary predictions about the existence of altruism [6].

In the previous section, I mentioned that it is often difficult to obtain clear-cut observational evidence about the level at which adaptations exist. But there is, in addition, a prior conceptual difficulty that needs to be overcome. It is embodied in the following simple argument:

- 1) Altruists are less fit than selfish individuals.
- 2) In a selection process, less fit characteristics decline in frequency, and more fit characteristics increase.

Altruism declines in frequency under natural selection.

The first premise of this argument seems simply to report how biologists define the concept of altruism. The second premiss simply reflects a fact about how models of natural selection understand the relationship between fitness differences and evolution. The puzzle is this: why has evolutionary theory debated the problem of altruism for so many years, if it can be resolved by so simple an argument? This argument says that altruism cannot evolve; it appeals to no observational fact about specific populations or organisms. Unless the entire history of this problem has been a wild goose chase, there must be a defect in this little deduction.

The problem is with premiss (1). It does not accurately reflect how altruism should be defined. What is true is that altruists are less fit than selfish individuals *who live within the same group*. But it does not follow from this that altruists will be less fit than selfish individuals *in the ensemble of groups*. To understand the problem of altruism, it is important to see why this claim about the ensemble does not follow from what is true for each group in the ensemble.

This may sound absurd and paradoxical. Indeed, *it is entirely natural to think that what is true within each part also must be true within the whole as well*. This "reductionistic" idea about how wholes and parts are related is deeply ingrained in commonsense; nonetheless, it is wrong. The idea of group selection is hard to grasp because it requires that one overcome this commonsense prejudice.

Fig. 1 displays some of the main ingredients in the concept of evolutionary altruism. The fitnesses of the two traits S (for selfishness) and A (for altruism) are each shown as a function of the composition of the group. Notice that no matter whether altruism is common or rare in a group, selfish individuals are on average fitter than altruists. The broken line represents the average fitness

(\bar{w}) of individuals in the group. This may be thought of as a measure of the group's fitness; the group produces more offspring if the average fitness of the individuals in it is greater. Notice that groups of altruists are on average fitter than groups of selfish individuals. The numbers on the y axis are arbitrary fitness units; think of them as expected numbers of offspring if you like.

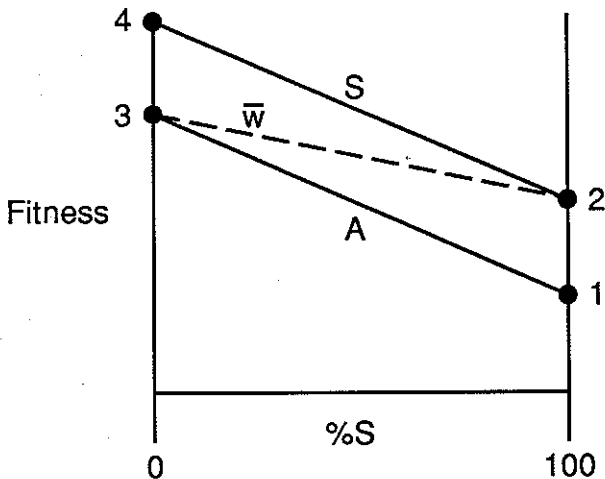


Fig. 1. Within any group, selfish (S) individuals are fitter on average than altruistic (A) individuals. However, groups of selfish individuals are less fit on average than groups of altruists.

To illustrate the idea about wholes and parts that I just mentioned, let's consider a simple example. Suppose we have two groups, each containing one hundred individuals each. Group 1 is 1% selfish; group 2 is 99% selfish. The approximate fitnesses of the traits, both within each group and averaged across the two groups, can be extracted from Fig. 1:

Group 1	Group 2	Global Average
(1) $w_S = 4$	(99) $w_S = 2$	$w_S = 2$
(99) $w_A = 3$	(1) $w_A = 1$	$w_A = 3$

Notice that what is true within each group is *not* true within the ensemble of groups. Selfishness is fitter than altruism within each group, but the reverse is true within the ensemble.

Statisticians have known about this phenomenon for a long time; it is called *Simpson's Paradox*. Without Simpson's paradox, altruism cannot evolve. A failure to appreciate the significance of Simpson's paradox makes the falla-

cious argument displayed before look utterly compelling. A simple syllogism makes a biological problem seem as if it can be settled by a definition.

Fitness is a quantity that allows one to compute next generation frequencies of a trait from frequencies in the present. Assuming clonal reproduction and non-overlapping generations, how will the frequencies of *S* and *A* change, both within each group and across the ensemble of groups? The numbers are as follows:

	Group #1	Group #2	Global Average
now:	S=1%	S=99%	S=50%
next generation:	S=1.3%	S=99.1%	S=27%

Selfishness increases in frequency within each group, but declines in frequency in the ensemble.

If common sense enshrines the reductionist idea that what is true within each part must also be true within the whole, even more does it sanction the idea that the *direction of change* in each part must automatically produce the same directional change in the whole. If Democrats are declining in frequency in each state of the Union, doesn't it follow that Democrats are declining in frequency in the United States as a whole? The answer is *no*; it is essential to see this, if one is to be able to grasp even the possibility of the evolution of altruism.

Notice a few vagaries in the example I have discussed. I began the system at 50% altruism, and with like for the most part living with like. Also, I traced the evolution of this system for one generation only. This is, so speak, to look at the system in mid-stream. How did altruism manage to reach the 50% mark? Why is it that similar organisms are living together? And what will happen if the system is allowed to evolve for many more generations?

Let us take the last question first. If the fitness units displayed in Fig. 1 are expected numbers of offspring, then both groups are growing in size. If the two groups hold together indefinitely into the future, each will grow fatter and fatter. Within each group, selfishness is increasing in frequency. In the limit, each group will approach 100% selfishness. In this case, we may safely conclude that the same fate awaits the ensemble of groups. Altruism will be eliminated from the ensemble, if the groups hold together.

To prevent this from happening, it is essential to have the groups reproduce. They must produce offspring colonies. If the groups fragment often enough, and if fitter groups found more offspring colonies than less fit groups, then altruism can be stably maintained in the ensemble.

Alternatively, we could somewhat change our interpretation of the

organismic fitness values, and allow groups to go extinct. If groups with many selfish individuals go extinct more often than groups that contain lots of altruists, this may provide a group-level process that helps counteract the individual selection occurring within each group that works against altruism.

Another question mentioned was why similar organisms are living together in the little example I presented. A simple biological device to ensure this is to have relatives live together. Sometimes kin selection is equated with individual selection. My inclination is to see kin selection as a kind of group selection, in which the groups are made of relatives.

The reason I find this apposite is that relatives can compete with each other just as much as nonrelatives. If sibs live together, selfish sibs will do better than altruistic sibs within the group. The fact that they happen to have the same parents does not affect this point. What determines an organism's fitness is its phenotype, not its pedigree [7]. When groups are composed of relatives, it still is true that the within-group process works against altruism. To counteract this, one needs a between-group selection process. This is why kin selection is appropriately construed as a form of group selection.

I hope it is clear from all this that the existence of altruism cannot be settled by a *a priori* argument. Rather, what is relevant is the biological properties of the system under study. One needs to have an ensemble of groups that differ in their local frequencies of altruism and selfishness. The groups must go extinct and found colonies sufficiently often to counteract the within-group process that promotes selfishness. It is possible that some natural systems should obey these requirements whereas others may not. The evolution of altruism is ultimately a question about population structure.

III. THREE RED HERRINGS

Having said this, I want to identify three red herrings that have distracted biological discussion from the appropriate empirical questions. Williams [3] argued that group selection hypotheses are "unparsimonious" and so should usually be rejected in favor of lower-level selection hypotheses. Dawkins [2] repeats this argument.

Maybe it is true that the kind of two-tiered process I have just described is "more complicated" than straightforward Darwinian selection within the confines of a single population. This may be right, but I can't see that it matters. The question is which sort of model of selection is more realistic and plausible; parsimony has nothing much to do with this [8].

Perhaps there is some sense to the idea that the requirements for the evolu-

tion of altruism are so constraining that they will rarely be satisfied in nature. If this is right, then a population drawn "at random" from nature will probably not contain altruistic characteristics [9]. This argument, it is important to see, rests on a biological premiss, not simply on an *a priori* principle of methodology.

A second red herring is the idea that genes, not groups, must be the units of selection because genes are the units of heredity. This simply doesn't follow, if "unit of selection" means the level at which adaptations accumulate. In the previous discussion, I talked about *A* and *S* as phenotypes of organisms. The discussion would have been no different if I had said that *A* and *S* are genes in a haploid organism. If the *A* gene evolves, this must be because there is sufficient between-group selection to balance the (within group) individual selection that works against it. Defenders of group selection hypotheses do not doubt the correctness of Mendelism.

A third red herring is provided by the following argument: The gene, not the organism or the group, must be the unit of selection, because all selection processes can be represented in terms of allelic fitnesses and frequencies. Again, there is a sense of "represent" according to which you can provide genic descriptions of selection at any level. If gene frequencies change owing to natural selection *at any level whatever*, there will be variation in the average fitness of the genes. However, this has nothing to do with the question of what sort of selection process is occurring.

A variant of this variant, defended by Sterelny and Kitcher [10], argues that it is a matter of convention whether we say that the gene or the group or the organism is the unit of selection, again on the grounds that a genic representation is always available (though the same cannot be said for higher-level representations). I grant that it is a matter of convention how we choose to describe the biology, in the sense that various mathematical formalisms may each have their utility. But what is not conventional is the biological process itself [11]. Whether altruism evolves is not a matter of convention (unless everything is a matter of convention!).

I do not reject the utility of thinking about evolution from the point of view of genes. A genetic model is obviously very important to understanding an evolutionary process. When biologists talk about phenotypes, and model an evolutionary process accordingly, they are basically assuming that the phenotypes are heritable—roughly, that phenotypes and combinations of genes are correlated. This is what I did before when I initially treated *S* and *A* as phenotypes, but then shifted to thinking of them as genes.

IV. HOW HIGHER- AND LOWER-LEVELS OF SELECTION
ARE RELATED

In models of group selection that involve altruism, selection occurs *within* groups as well as *between* them. Different groups have different productivities; and organisms in the same group also have different productivities. The interaction of these two sorts of process determines the trajectory of the system as a whole.

Precisely the same thing can happen between and within organisms. Organisms can survive and reproduce to different degrees. And inside an organism, some genes may be more reproductively successful than others. Characteristics evolve because of the interaction of these two sorts of processes.

Before describing the within- and between-organism analog of group selection, I want to reformulate the description I gave in the previous section of how group selection works. I'll continue to talk about traits *S* and *A*, but now, for the sake of generality, I won't always mean selfishness and altruism by those letters.

Suppose that organisms live together in groups of four. This means that there are five possible group compositions, ranging from *SSSS* to *AAAA*. Assume further that a group's productivity is an increasing function of the number of *A* individuals it contains. The fitness functions of the five group types are displayed in the left-hand column of Fig. 2. This describes the between group part of the selection process [12].

We now may ask what happens within each group. We can compute this (assuming a haploid model) by describing the percentage of *A* offspring that are produced within groups of different compositions. Different assumptions about this are represented by the right-hand column of Fig. 2.

In the first row right column, the frequencies of *A* and *S* types in the offspring generation are precisely the same as the frequencies in the parental generation. This means that *S* and *A* are equally fit within each group. So the first row of Fig. 2 represents a case in which there is between group selection favoring *A* and no within group selection at all. The result is that *A* will go to fixation.

In the second and third rows (right column), we see represented the idea of within group selection against *A*. Note that the offspring frequency of *A* is always *less* than the parental frequency, if both *S* and *A* are present in the same group. This means that *S* individuals are producing more offspring than *A*

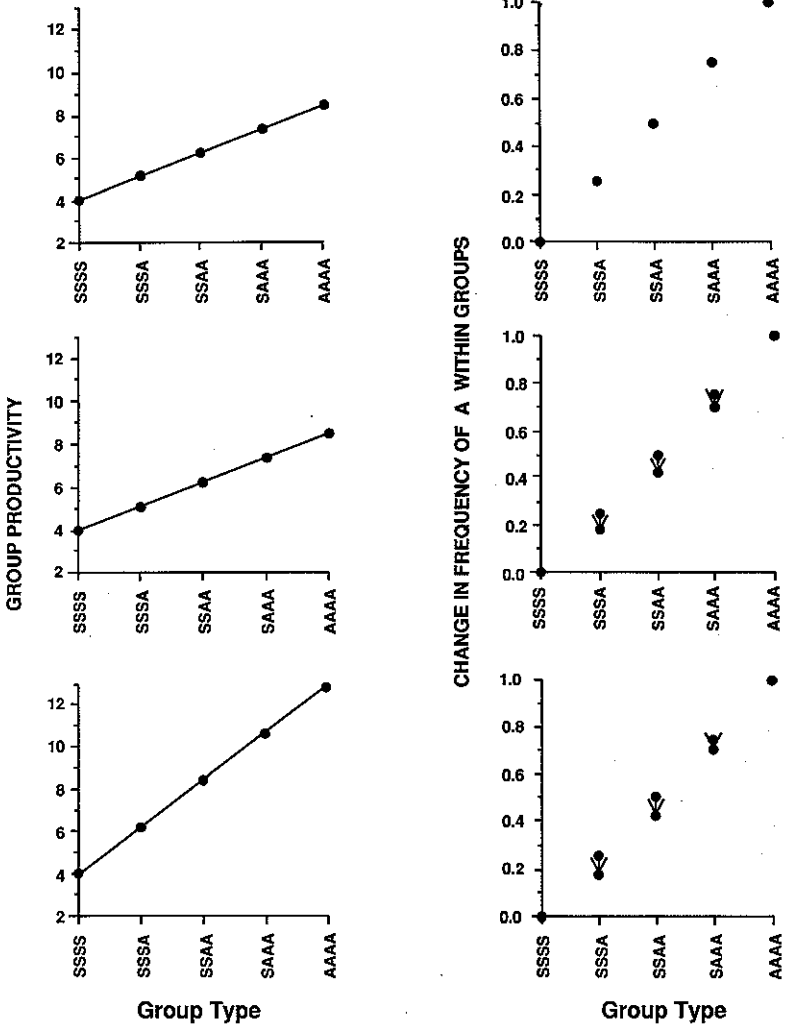


Fig. 2. The left-hand column shows how a group's productivity is influenced by the percentage of A individuals it contains. The right-hand column shows whether A individuals are less reproductively successful than S individuals within the same group. Line 1 depicts group selection favoring A, but no (within-group) individual selection, so the result is that A goes to fixation. Lines 2 and 3 describe a conflict between group selection favoring A and individual selection favoring S. The fate of the population is determined by the relative magnitudes of these two forces.

individuals in the same group. So in both the second and the third rows of Fig. 2, there is between group selection favoring *A* and within group selection against *A*.

What will be the result? Since the within group components are the same in these two cases, the result depends on the magnitude of the between group selection. Note that there is more between group selection in row three than there is in row two; the slope of the between-group line is greater in row three than it is in row two. In row two, the within group component of selection is sufficiently powerful to overwhelm the between group process; the result is that *S* goes to fixation. However, in row three, the result is a polymorphism, with both *S* and *A* stably maintained in the ensemble.

In Fig. 3, the comparison of between- and within-group selection is transposed to allow us to compare between- and within-organism selection. The left-hand column describes some standard representations of one locus, two allele models. In row one, *aa* individuals are less fit on average than *Aa* individuals, who in turn are less fit than *AA* individuals. In row two, left column, there is no variation in fitness between individuals. And in rows three and four (left column again), organisms with different genotypes differ in fitness.

The right-hand column of Fig. 3 represents what happens within organisms. We now ask what percentage of *A* gametes each of the three genotypes produces. In the top row (right column), we see the result of a "fair" Mendelian process. The heterozygote produces 50% *A* bearing gametes and the two homozygotes produce 0% and 100%, respectively. This cell describes a case in which there is no within organism selection. Here we are thinking about the genes at a locus (or the gametes or chromosomes in which those alleles occur) as parts of an organism, just as earlier we thought of organisms as parts of a group.

Rows two through four, right column of Fig. 3, describe the process of *meiotic drive*. In this case, the fair Mendelian meiotic ratio is subverted; heterozygotes produce fewer than 50% *A* gametes. A selection process is at work within such organisms; genes (or chromosomes or gametes) are competing with each other. This is precisely analogous to rows two and three (right column) in Fig. 2, in which heterogeneous groups are such that *A* organisms do less well than *S* organisms.

Let's now consider what the result is of the four processes described in Fig. 3. In row one, there is between organism selection but no within organism selection; the prediction of this standard one locus two allele model is that *A* will go to fixation. In row two, there is no selection between organisms, but

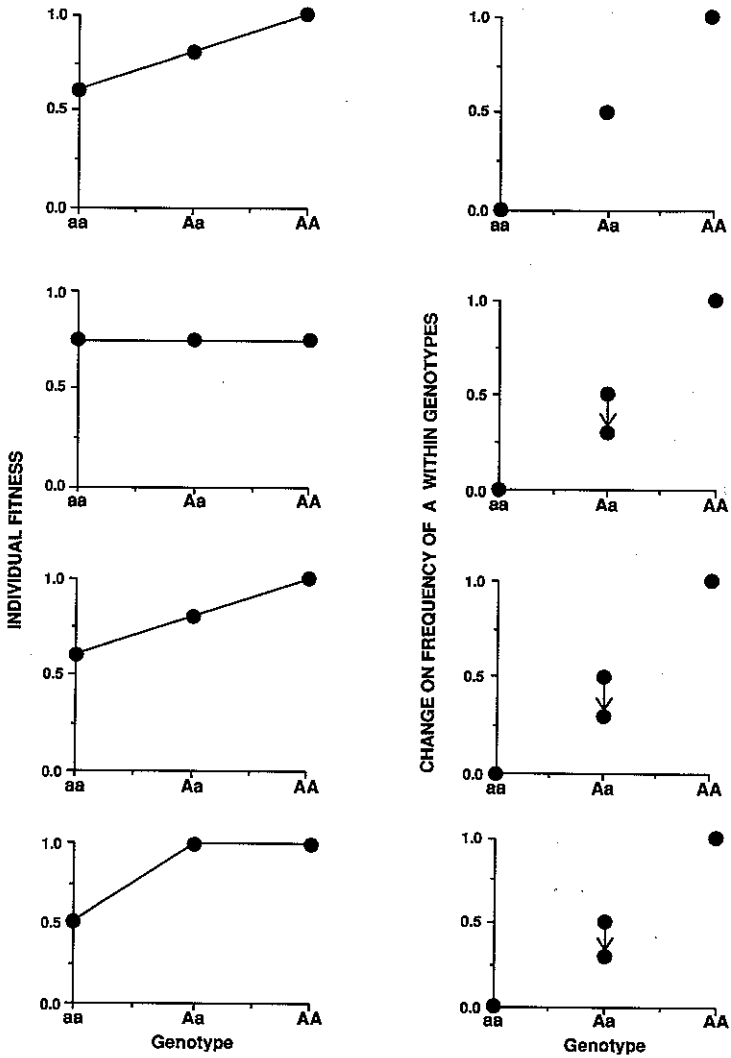


Fig. 3. The left-hand column shows how an individual's fitness is influenced by the percentage of A genes it contains. The right-hand column shows whether A genes are less reproductively successful than a genes within the same individual. Line 1 depicts individual selection favoring A, but no meiotic drive, so the result is that A goes to fixation. Lines 2 and 3 describe a conflict between individual selection favoring A and meiotic drive favoring a. The fate of the population is determined by the relative magnitudes of these two forces.

meiotic drive occurs; this form of within organism selection causes a to go to fixation. In rows three and four, there is both between organism selection (favoring A) and within organism selection (favoring a). The magnitude of the segregator distorter effect is the same in both cases; what distinguishes the two rows is the magnitude of the between organism effect. In row three, a goes to fixation; meiotic drive is "stronger" than the opposing between organism selection. In row four, a polymorphism evolves; the two opposing forces are more nearly in balance.

Some useful lessons flow from placing Figs 2 and 3 side by side. First, no absolute claim can be advanced about what will happen when a higher-level selection process is opposed by a selection process at a lower level. When between group and within group selection oppose each other (lines two and three of Fig. 2), the result can be a polymorphism or fixation of the trait favored by the lower-level process. When between organism and within organism selection oppose each other (lines three and four of Fig. 3), the same two options are available. It is an oversimplified reductionism that claims that the result of such processes is always determined by the lower-level component.

If we find ourselves too much at home in the Darwinian framework of adaptations that exist for the good of the organism possessing them, the parallelism between these two figures may provide a useful corrective. If it strikes us as natural and inevitable that group adaptations rarely if ever evolve, we also need to ask why organismic adaptations are so commonplace. For just as what is good for the group can be subverted by what is good for the organism, so what is good for the organism can be (but need not be) subverted by what is good for the gene. If organisms are functionally integrated, with parts working for the good of the whole, this is a fundamental fact about the living world that demands explanation. To see it as natural and inevitable is to miss the fact that this is a contingent truth that requires explanation.

A segregator distorter gene that has a strong distortion effect will go to fixation, even though its average effect on organisms is deleterious, if the effect on organisms is, so to speak, less severe. In this case, what evolves will be bad for organisms, but good for the truly selfish genes themselves. The more loci for which this is true, the less apt it will be to regard the organism as the preeminent level at which adaptations have accumulated. Rather, traits that happen to be good for the organisms possessing them merely constitute fortuitous organismic benefits; they will not be organismic adaptations.

We may put the point the other way around. What sort of circumstance is most conducive for the evolution of higher-level adaptations? "Higher level"

is here used as a relative notion. We are asking simultaneously how to get organismic adaptations rather than genic adaptations, and how to get group adaptations rather than organismic adaptations. One thing that helps this happen is the suppression of selection at the lower level. If there is no variation in fitness at lower levels, then only higher-level biases can direct the process. In the within- and between-organism case, this means the suppression of meiotic drive. Organisms may evolve modifier genes that reduce segregation distortion. Or, alternatively, segregation distortion may be allowed to do its work, after which point new allelic variation is introduced that is not vulnerable to the driving genes.

The other way to allow higher-level adaptations to evolve is to increase the strength of the higher-level selection process. An altruistic characteristic is better able to evolve if it dramatically increases the fitness of the group in which it occurs, rather than just modestly augmenting it.

Allee and Emerson *et. al.* [13] and Wynne-Edwards [14] thought that group adaptations were to be found in long-lived groups. These groups were able to persist for so long precisely because the organisms in them are altruistic. More recent quantitative modelling has shown that long-lived groups are not at all the best places to look for group adaptations. Groups that hold together for a long time allow selfish individuals to displace altruists. What helps altruism to evolve is groups that are *short-lived*.

We often think of traits that extend the lifespan of an organism as organismic adaptations. This may be true, but the present point is that such traits can provide a less than optimal setting for other organismic adaptations to evolve. For a long-lived organism is a being in which selfish genes have more time to displace genes that benefit the organism at their own expense. Organisms are remarkable kinds of things. There is no *a priori* reason why so much of the earth's adaptations should be devoted to their needs. To the degree that the organism is the preminent (if not the only) unit of selection, this fact is a very important one to explain.

V. INDIVIDUALS AND UNITS OF SELECTION

The idea of individuality has recently had a large impact on some questions in systematics. In this section, I want to describe how this concept is related to the units of selection problem. It is sometimes thought that the idea that *species* are individuals entails that species are units of selection. Conversely, Hull [15] has argued that a unit of selection, at whatever level it exists, must be an individual.

Ghiselin [16] and Hull [17] advanced the idea that species are not natural kinds, but are spatio-temporal individuals. This is a claim with two separate parts, and so two different arguments are needed to establish it.

A natural kind is definable by some property that all and only the members of that kind must possess. More specifically, that property must leave open where and when the instances of the kind can be found. So, for example, *gold* is a natural kind, defined by its atomic number. The lumps of gold that populate the universe may be scattered anywhere; and as far as the definition is concerned, they may exist at any time.

A biological species, on the other hand, does not possess a characteristic that is both necessary and sufficient for membership in it. This part of the individuality thesis continues Hull's [18] war against essentialism. In addition, membership in a species requires a physical connection with other organisms who also are in the species. If there were organisms in some distant galaxy that are physically just like tigers, they would not *be* tigers, according to Ghiselin and Hull, if they have no historical connection with terrestrial tigers. This is why species are not natural kinds.

A number of commentators have realized that it takes more to show that species *are* individuals than showing that they are *not* natural kinds [19]. Consider the purple objects that are within a hundred miles of Paris and whose entire existence falls between the years 1950 and 1990. Call any such object a PURPLE, for short. Each PURPLE is an individual, but there does not seem to exist an individual of which they (and only they) are the parts. In general, an arbitrary assemblage of individuals does not comprise an individual. Yet, the PURPLES bear relationships to each other; and the definition of the PURPLES imposes a spatio-temporal restriction. What, then, prevents this "whole" from being an individual?

The natural answer is that the parts of an individual must causally interact with each other in ways that they do not interact with things outside the individual [20]. Organisms are paradigm individuals; organ systems and cells causally interact with each other in ways that they do not interact with things outside the organism. This figure/ground contrast between "self" and "nonself" is important. It isn't enough to require that the parts of an organism causally interact with each other. That is too weak, because every physical object exerts a gravitational force on every other. This is true for all the PURPLES. The reason the PURPLES don't constitute an individual is that they are not doing anything with each other that they aren't also doing with things outside.

Typically, the parts that comprise an individual will be physically

contiguous; again, familiar organisms provide our paradigm. But this is not strictly necessary. As Ghiselin has noted, the United States of America is an individual nation state, even though its constituent states are not physically contiguous. The key point is that the states interact with each other in ways that they don't interact with things outside.

The United States is a *political* entity. This tells us, roughly, what sorts of interactions we are to expect to occur within nations but not between them. Now let us consider *species*. To say that they are individuals requires more than simply that their parts be genealogically connected. After all, the entire tree of life is genealogically connected, but it doesn't constitute one big species. So what physical interactions carve out the species?

Hull and Ghiselin have opted for the Mayrian [21] idea that reproduction is the cohesive force that binds together the parts of a species. Organisms (or populations) in a species exchange genetic material to produce offspring. Organisms in the species do not do this with organisms that are outside [22].

An immediate consequence of this idea is that there are no asexual species. The organisms in an asexual species often have no more to do with each other than do organisms in different species that happen to belong to the same genus or family. They have a common ancestor, but they go their own ways. Asexual species and higher taxa might perhaps be called "historical entities" to distinguish them from natural kinds [19]; but they aren't individuals.

Another consequence of this proposal is that it appears that many so-called sexual species are not species at all. Species are often made of semi-isolated local populations. If migration between local populations binds the populations to each other genetically, then they will form good individuals. But if there is no gene flow, then these parts are not causally connected with each other in the requisite way [19]. Of course, it is an empirical question how much gene flow there is.

Ghiselin and Hull have accepted these consequences of their proposal. They are prepared to deny the existence of asexual species and to withhold the species appellation from sexual meta-populations in which there is no gene flow between subpopulations. I won't discuss the plausibility of these conclusions; rather, I want to identify the connection of the individuality thesis with the units of selection problem.

Species selection is an idea that was introduced in connection with the idea of punctuated equilibria. But here again we must be careful. The idea of punctuated equilibrium is a claim about when change occurs in the lifetime of a species; it says that most of the change occurs early on, with the species remaining relatively static thereafter. This claim says nothing about the causes

of speciation, or about why some clades contain more species than others. It is to the latter idea that the hypothesis of species selection pertains. In brief, punctuated equilibrium is a claim about *pattern*, whereas species selection is a claim about *process*.

The rough idea behind species selection is that there is a nonrandom process by which some species give birth to daughter species more often than others do. Species reproduce differentially, in a way that cannot be accounted for as the upshot of purely organism-level selection [23].

One question about the relationship of the individuality concept to the idea of species selection is easy to answer. A good Mayrian species will be an individual. But this does not require that any sort of species selection should have taken place. Mayrian species are perfectly at home in the framework of strict Darwinian organismic selection. The individuality of species does not entail that they have been units of selection.

The relationship in the other direction is a bit more subtle. Does the idea of species selection require that species be individuals? I think the answer to this question is *no* as well. Consider the case of a so-called sexual species whose local populations do not exchange genetic material with each other. This "species" is not an individual in the sense required by Ghiselin and Hull. However, there is no reason why a set of such "species" should not have different propensities to speciate. This would be species selection, but without the species being individuals.

It is important to recognize that the idea of individuality comes in degrees. Organisms may vary with respect to how mutually dependent their parts are on each other. Tigers are better individuals than a field of dandelions connected by underground runners. The parts of a tiger show a great deal more functional integration than do the parts of this dandelion network. Kill a part of the tiger and the rest of the tiger may die as well; this is not nearly so true for the dandelion.

Although organisms may differ in the degree to which they are "individuals," it is perfectly possible that different degrees of individuality should have evolved by straightforward Darwinian organismic selection. The high degree of individuality found in tigers may be the result of individual selection; the same may be true of the lower degree of individuality found in dandelions. Functional interdependence of parts may be advantageous for some organisms, but disadvantageous for others. Varying degrees of individuality may be varying responses to the pressures of individual selection.

Some groups are far more functionally integrated than others. And two groups may both display high degrees of functional integration, but for histor-

ically quite different reasons. A Mayrian species shows a great deal of interdependence between the two sexes. A eusocial colony of insects may also display a high degree of functional integration. However, the causal explanation may be quite different in the two cases. If sexuality has an explanation in terms of organismic selection, then the functional integration of sexual populations will be an artifact of lower-level selection, not a species-level adaptation. On the other hand, the functional integration of some haplo-diploid species may be due to competition between groups.

In short, individuality is a way of characterizing the present configuration of an object, whether that object happens to be an organism, a group, or a species. Individuality comes in degrees, depending on how much the parts of the object depend on each other. In contrast, the idea of a unit of selection describes the history of an object, not its present configuration. The individuality of an object may have different possible explanations; and two objects may have evolved different degrees of individuality as the result of selection at the same level. Selection at a given level of organization does not have to produce objects at that level that are highly individualistic. And an object at a given level may be highly individualistic even though it is not the result of selection at that level.

VI. CONCLUDING REMARKS

Organisms are marvelously well-adapted entities. Darwinian selection between organisms is an attractive, if not exclusive, mechanism for explaining why organisms are the way they are. But to simply say that a trait evolved because it was advantageous for the organism possessing it is to gloss over a complication that any adequate theory of adaptation must address.

Organisms are made of parts. If evolution largely suppressed competition between parts and produced organisms whose parts behave in a highly cooperative manner, why did this happen?

Organisms are themselves parts of larger wholes. If evolution has allowed organisms to compete with each other, instead of forcing them to cooperate in the interests of the wholes to which they belong, why did this happen?

Since the adaptive interests of objects at different levels of organization can come into conflict, an adequate adaptationism must say whether and why different levels of organization managed to accumulate characteristics that furthered their interests in surviving and reproducing.

Individuality—the tight integration and interdependence of the parts of a whole—is one of the major results of evolution. We find its preeminent

examples at the level of organisms. This does not mean that all organisms are individuals to the same degree; nor does it mean that objects at other levels are always wholly lacking in individuality. A major project for evolutionary theory is to explain the variation in degree of individuality that we find within and between levels.

University of Wisconsin

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6. The fact that altruism is an important test case does not mean that individual and group selection must oppose each other. As I’ll explain shortly, group and individual selection can work in the same direction. And it also is possible to have group selection without any individual selection at all.
7. I also should mention that some models of group selection allow altruism to evolve even when groups are randomly assembled. See Wilson (“Weak Altruism, Strong Group Selection,” *Oikos* 59 (1990) 135–40) for discussion.
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9. Wade, *op. cit.*, reviews a number of quantitative models of group selection that claim to establish this sort of thesis; Wade argues that the models in various ways *a priori* bias the case against group selection.
10. Sterelny, K. and Kitcher, P. [1988]: "The Return of the Gene." *Journal of Philosophy* 85: 338-61.
11. Compare: (i) It is a matter of convention whether we use the words "dogs have four legs" to express a truth rather than a falsehood; (ii) it is a matter of convention whether dogs have four legs. I accept (i) but reject (ii). (i) embodies the idea of "trivial semantic conventionalism."
12. Figures 2 and 3, and the idea of using them to illustrate the parallelism of between/within group selection and between/within organism selection, are due to D. Wilson, "Weak Altruism, Strong Group Selection," *op. cit.*
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