ABSTRACT. This paper inquires into the very possibility of the units of selection debate's origin in the problem of altruism, function in articulating the evolutionary synthesis, and philosophical status as a problem in clarifying what makes something a level or unit of selection. What makes the debate possible? In terms of origins, there are a number of logically possible ways to deviate from the model of Darwinian individual selection to explain evolved traits. In terms of function, adherence to the evolutionary synthesis yields norms which restrict these possibilities to a manageable few. In terms of philosophical status, the abstract structure of selection mechanisms permits a causal construal, on which the unit of selection is identified with the "unit of possession", that which possesses the causally efficacious trait selected for. It also allows a teleological interpretation, on which the unit of selection is identified with the "unit of benefit", that for the sake of which the causally efficacious trait is selected. It is proposed that a unit of selection is really a pair of units, consisting of both a unit of possession and a unit of benefit.

Why is there a philosophical controversy over genic selection, individual selection, and group selection? Like other "Why?" questions, there are several correct answers, depending on what sort of answer is presupposed in the asking. We might mean, "What motivated the debate?", a question about its origin. We might mean, "What is the debate's function?", a question about its import for evolutionary biology. Or we might mean, "What gives the debate its philosophical status?", a question about its philosophical significance. More fundamental and controversial than any of these is a further question which has been neglected in the literature on the units of selection. For we might mean, "What makes the debate possible?", a question about how there can be such a debate at all.

The first step toward understanding how the debate is possible is to decide what considerations we are willing to accept as relevant. It is reasonable to suppose that how we answer questions about the debate's origin, function or philosophical status has some bearing on a proper answer to our question about the debate's possibility. The task of this paper will be to decide what bearing those questions do have. The method of exposition, then, will be to consider in turn the implications
of the debate's origin, function, and philosophical status for its very possibility. I hope to show that addressing the possibility question in this way helps us gain a more adequate view of the units of selection problem by calling attention to the roles of causal and teleological reasoning in the debate and to related presuppositions about what a unit of selection is.

1. The Debate's Origin and Possibility

The motivational origin of the debate is found in the felt need to explain how altruism, assumed to be central to animal and human societies, could be promoted by natural selection. That much is widely known. Yet largely unrecognized is the fact that responses to the altruism problem incorporated several attitudes about what a unit of selection is. It is viewed as a unit of benefit, relating to what objects are benefited by selection mechanisms. It is viewed as a genetic unit, relating to apparent selfishness or altruism as different means toward the end of genetic selfishness. It is viewed as a teleological unit, relating therefore to what ends traits are designed by selection to accomplish. Let us see how these related views arose.

Darwin and Wallace recognized that altruism is a problem for their theory. Darwinian individual selection (hereafter, DIS) promotes traits benefiting their possessors at the expense of other individuals in the population. Altruistic traits benefit others at the expense of their possessors. Hence, the evolution of altruism cannot be explained by DIS, or so it seems. Of course, a trait good for its possessor is by that fact also good for the species in a minimal sense merely in virtue of the individual's being a part of its species. So Darwin held that traits good for others or for the group which are also good for their possessor could be explained by DIS. Wallace was willing to accept much more readily than Darwin the postulation of group selection for group-benefiting adaptations in cases difficult to explain by DIS.

The Darwin-Wallace exchange gave evolutionists a legacy of preconceptions about selection which are still influential today. First, understanding selection rests on a distinction between what I shall call the "unit of possession" and the "unit of benefit". In their exchange individual and group selection involve the same unit of possession: the traits selected for are possessed by individuals. But they involve different units of benefit: the traits selected for in DIS benefit the individual possessing them whereas the traits selected for in group selection benefit the group of their individual possessor. So, second, the unit of selection is identified with the unit of benefit rather than with the unit of possession. Even though it is possible to view traits benefiting both the individual and the group as being subject to both individual and group selection, the altruism problem led to a third view: group selection is restricted to promoting traits selected against by individual selection.

The current units of selection debate took off from the exchange between Wynne-Edwards and Williams. Neither questioned the presuppositions just described. Wynne-Edwards (1962) noticed that even though the trait of self-imposed restrained breeding hurts the individual's relative reproductive success within its population and thus is selected against by DIS, populations full of such altruists are less likely to go extinct than populations of maximally breeding selfish individuals (which
over-exploit their food resources due to over-population). Thus the prevalence of self-imposed birth control would reflect the balance and relative strength of DIS against the trait and group selection for it. Wynne-Edwards' contribution was not only to drive home the point that explanations of the evolution of a trait "because it is for the good of the species" require postulation of a group selection mechanism, but also to raise consciousness of the need to explain altruism and social behavior in general. Williams (1966) played the modern Darwin to Wynne-Edwards' Wallace, arguing that no group selection mechanism is ever needed (with some possible exceptions, e.g., the house mouse t-allele). Apparent cases of altruism with group-benefiting adaptation can almost always be explained away as incidental effects of DIS, e.g., the trait is not really altruistic or, if altruistic, it did not evolve because of its benefit to the group. Williams' contribution was to raise the critical standards for explaining adaptation but with the unfortunate effect of convincing a generation of ecologists that any hypothesis congenial to group selection is either false or to be viewed with suspicion.

Both sides tended to accept a restrictive dichotomy: all selection is either DIS or group selection. To transcend this dichotomy selection had to be understood so as to combine Darwinian and Mendelian ideas. The evolutionary synthesis of Darwinism and Mendelism had played only a minimal role in the debate so far. Even genetic arguments against the ability of group selection to effectively counteract DIS, such as those showing that altruistic groups would rapidly become selfish groups due to subversion from within by selfish cheaters, could be made in natural history terms without essential reference to genetics. Essential reference to genetics occurred by bringing to the fore the concepts of genotype and phenotype which Darwin had been unable to formulate in his speculations on heredity. His allowance for Lamarckian inheritance of acquired traits violates the fact that the genotype is virtually constant during an individual's lifetime despite continual fluctuations in its phenotype. The new genetic orientation would lead to viewing the unit of selection as a genetic unit.

DIS favors those traits which benefit their possessor's self-interest. But what is the organismic self? From an evolutionary genetic perspective, organisms differ from other complex physico-chemical systems (Michod, 1983) in that they have two layers of self. They have a genotype consisting of inherited genes and a phenotype consisting of traits arising from gene-gene and gene-environment interactions during development. Individual selection dictates that organisms act in their own self-interest, but this demand only extends to the genotypic self and not to the phenotypic self. We distinguish selfishness/altruism of the genotype and of the phenotype as follows. "Phenotypic selfishness" means behavior by which an organism increases its chances for reproductive success (its Darwinian fitness) and decreases those of at least one other organism in the population. "Phenotypic altruism" is defined similarly but with the unit of benefit reversed. "Genotypic selfishness" means behavior by which an organism increases its chances for perpetuating genes identical in kind to its own (its genetic fitness) and decreases those of at least one other organism in the population. "Genotypic altruism" is defined similarly but with the unit of benefit reversed. Notice that the (means-end) relation between behavior and fitness implicit in the "by which" locutions here incorporates a teleological orientation.
Such definitions allow us to break out of the dichotomy on which all selection is either DIS or group selection. Selection for behaviors which are both phenotypically altruistic and genetically selfish is not expressible in a model of DIS, in the strict sense of lacking the genotype-phenotype distinction. But it counts as individual selection according to the criterion that the unit of selection is the unit of benefit, i.e., phenotypic altruism is selected for when it better perpetuates the organism’s genes than does phenotypic selfishness.

This conceptual reorientation inspired the development of a number of different mechanisms promoting phenotypic altruism. Some followed Wright’s (1945) model of selection in a sub-divided population depending on either differential production of migrants by sub-groups or differential extinction of sub-groups. Others discarded the assumption of selection between reproductively isolated groups (demes) for that of selection of groups within demes. The best critical review of these models and their assumptions is that by Wade (1978), who reviews seven models of interdemic group selection and five models of intrademic selection. Maynard Smith (1982) discusses the differences and similarities of other mechanisms classified under the headings of interdemic selection, kin selection, synergistic selection, and reciprocal altruism. Further developments include theories of sexual selection, the evolution of sex, parental investment, parental manipulation, and sex-ratios. The debate over individual versus group selection is considerably complicated by this proliferation of selection mechanisms, giving us the debate as we know it today.

To summarize. The Darwin-Wallace exchange over altruism gave us the presupposition that the unit of selection is a unit of benefit. The Wynne-Edwards-Williams exchange eventually culminated in a distinction between genotypic and phenotypic altruism/selfishness, which gave us the presuppositions that the unit of selection is a teleological unit and a genetic unit.

What bearing does the origin of the units debate in the altruism problem have on its possibility? Consider E.O. Wilson’s illustration of how socio-biology uses the units problem to illuminate human nature. Why do we have ambivalent emotions during stressful situations? Wilson says (1975, 4) that the blends of love and hate or aggression and fear we experience are “designed not to promote the happiness and survival of the individual, but to favor the maximum transmission of the controlling genes”, “as a result of the balance of counteracting selection forces at different levels of organization”. Using as examples the individual, the family, and the tribe, he notes that “what is good for” or “preserves” or “promotes” objects at one level of organization may be “destructive to” or “weaken” objects at other levels (1975, 4). The answer suggested by or implicit in these remarks to our question, “What makes the units debate possible?”, is that it is possible for there to be conflicts of interest at various levels. We should not be surprised to find Wilson’s language incorporating presuppositions about what a unit of selection is which make sense in the light of the altruism problem. It concerns the level of objects a trait “is good for”, i.e., a unit of benefit. It concerns “the maximum transmission of controlling genes”, i.e., a genetic unit. And it concerns whose interests the trait is “designed” by selection to favor, i.e., a teleological unit.
The conflicts-of-interest thesis is widely held. Yet this cannot be the whole answer. For the debate arises in virtue of the relation between the possibility of conflicts of interest and DIS. No debate over altruism would be possible if it were not a problem for DIS. By "no debate" is meant "no debate as we know it today", complete with conceptual disputes arising from the proliferation of mechanisms deviating from DIS. To ask about the very possibility of the debate is not merely to consider what led up to it historically. It is to consider the range of conceptual disputes which have occurred since the debate began over what a unit of selection is and which levels count as units, and to ask of them how they are possible. We need to understand the possibility question this way to avoid trivializing it by making it answer-equivalent to the origins question. The possibility question turns on logically possible ways to deviate from the model of DIS.

Let us reconstruct the DIS model in its simplest form useful in this regard. Darwin inferred evolution by selection from superfecundity and inherited variation in fitness. If organisms are capable of reproducing more of their number than the environment can support and if some organisms have heritable traits which give them a better chance of reproductive success than other organisms possess in virtue of their heritable traits, then, within a population of such organisms, individuals with the more favorable variations will survive to reproduce at the expense of those with less favorable variations, and hence, the more favorable variations will be represented at a greater frequency in the next generation. As a result (given certain unspecified conditions), when the environment remains relatively constant the average fitness will gradually rise in the population, and when the environment dramatically changes one species of organism will gradually evolve into another species.

Suppose counterfactually that we know nothing of the altruism problem. A logical analysis of this DIS model should highlight the fact that on the model the same organism both possesses a heritable trait and benefits from it. With respect to any trait selected for we should distinguish the "unit of possession", that which possesses it from the "unit of benefit", that which benefits from it. Selection for altruism cannot occur on the model because it identifies the objects constituting the two units, i.e., the two concepts are assumed to be extensionally equivalent. The possibility of deviating from the model by letting different objects constitute the two units is what makes the very conception of selection for phenotypic altruism possible. But another way to deviate not involving selection for altruism is to keep the assumption that the objects constituting the two units are identical, but to disagree about whether these objects are always organisms. Objects at higher levels than the organism may both possess the trait selected for and benefit from it, e.g., species selection without altruism. Objects at lower levels may do the same, e.g., genic selection without altruism. The problem of (selection for) altruism, therefore, does not exhaust the debate. Many evolutionists think it does because they have not distinguished the origins question from the possibility question.

The conflicts-of-interest thesis is normally understood as parasitic on the altruism problem. So it is false that the debate is possible because of conflicts of interest. Rather, the problem of altruism and the debate in general is possible because of logical possibilities in saying
what objects count as units of possession or benefit. That is the fundamental source of the debate.

2. THE DEBATE'S FUNCTION AND POSSIBILITY

Another way to collapse the different meanings of our original "Why?" question is to identify the debate's function with the solution to the altruism problem. Suppose we accept the ordinary concept of function as requiring that something's function relates to its effect on a greater whole. The preceding point goes to show that the altruism problem is only part of the debate, not this greater whole. Hence, the debate's function cannot be to solve the altruism problem. What is this greater whole? We noticed that the character of the debate changed when both the Darwinian and Mendelian poles of the evolutionary synthesis were brought to bear on it. It is reasonable to identify this greater whole with the theoretical framework supplied by the synthesis. To use Kuhn's well-worn terminology, the debate's function is to "articulate" that framework. Framework-articulation is to be achieved by clarifying selection mechanisms, developing new mechanisms, and relating them to other mechanisms, to other theory, and to the actual world. For example, Boorman and Levitt (1980) connect the models of reciprocal altruism, kin selection, and group selection to the population genetics formalism of the synthesis and discuss their empirical applications.

What bearing does this function have on the debate's possibility? Consider Ruse's (1979, 13-15) introduction to the debate. He begins by saying that "an important question which must be asked about natural selection is precisely who benefits by it". He characterizes individual and group selection in a way which suggests that he is conceiving of a unit of selection as a unit of benefit. He goes on to point out that the interests of the organism and its groups may not coincide and gives some examples. This suggests adherence to the conflicts-of-interest thesis, at least as a pedagogical tool. Then he states the units problem:

The question of whether one can properly interpret characteristics as value to the individual but not (or only incidentally to) the group, or to the group but not (or only incidentally to) the individual, has troubled and divided biologists for many years. As also has the related question of whether one can properly distinguish an 'individual selection', promoting characteristics of value to the individual, from a 'group selection', promoting characteristics of value to the group (and if one can, whether both exist).

This statement of the problem obviously connects it with the altruism problem but may appear to have nothing to do with the synthesis. This appearance is misleading because Ruse's distinctions are important in virtue of their relation to the claims of the synthesis. We cannot protect the synthesis by making it compatible with all sorts of unforeseen views about selection. That approach threatens to trivialize it, making it "unfalsifiable" through redefinition by hindsight. One claim of the synthesis is that all or most evolution by selection is by individual selection, a claim of its Darwinian pole. Williams' (1966) efforts to show that group-benefiting adaptations are incidental and evolve as side-effects of individual selection articulated that claim. If group-benefiting traits were frequently non-incidental and had evolved by group
selection, or if group selection were able to overcome the effects of individual selection, or if we could not distinguish the two processes, the synthesis would seriously suffer. The word "distinguish" has both ontological meaning, relating to the objective distinctness of the two processes, and epistemological meaning, relating to our ability to find out whether important cases of selection are of individual rather than group selection. Let us consider first the ontological issue and then norms that relate to both it and the epistemological issue.

The debate is possible because, given the logically possible ways of deviating from the DIS model, it is an open question which differences serve as criteria for distinguishing individual from group selection. Examples abound. Given that the DIS model favors selfishness, one criterion is that group selection favors altruistic traits. That criterion is useless. First, Maynard Smith (1982, 30) classifies selection processes so that individual selection is never selection for altruism, which unduly restricts individual selection to the DIS model. As a result, many selection processes like kin selection, synergistic selection (within species mutualism), and reciprocal altruism are viewed as neither individual nor group selection. But most evolutionists view them as individual selection for good reason once we distinguish altruism/selfishness of the genotype and of the phenotype. Second, persuasive definitions identify group selection with selection for genotypic altruism. Since all selection is antecedently understood to be selection for genetic selfishness, these definitions rule out group selection by fiat rather than by argument. Third, group selection without altruism can occur when the same group is both the unit of possession and benefit, i.e., in the lab we choose a trait of groups conferring higher fitnesses on their possessor and select for groups with the trait.

Given that the DIS model only requires that individuals form a single population, a second criterion is the existence of more than one group. Thus Wade (1978) defines group selection as "that process of genetic change which is caused by the differential extinction or proliferation of groups of organisms". That criterion has many counter-examples. For any trait which directly or indirectly increases the chance of proliferation or decreases the chance of extinction would be promoted by group selection. In situations where individuals collect to form groups, individual selection may result in differential group fitnesses and therefore in group selection. Even those cases of incidental benefit to groups Williams argued to be explainable by individual selection, paradigm cases of naive group selectionist explanations, would count as group selection.

Given that the DIS model is silent on the relation between individual and group fitnesses, a third criterion for group selection is that group fitnesses and individual fitnesses show some dependence. On Wright's model of inter-demic selection, selection between individuals occurs in part because their fitnesses depend on what kind of group they are in. Fitter groups, ones at higher adaptive peaks, send out more migrants to other groups and take over those groups. But this is redescribable in terms of genetic drift, individual selection, and migration. By a "fitter group", Wright did not refer to some trait of a group, but only to a group such that the average fitness of its members is higher than that of other groups. His "group selection" is a statistical description of a case in which a trait of an organism becomes prevalent in a small semi-isolated deme by genetic drift (chance), organisms with that trait migrate into other such demes, and the trait becomes prevalent
there by individual selection. The lesson here is that any criterion which lets cases to which it is applicable be describable either as individual or as group selection has missed the difference.

Given that the DIS model is silent on population structure, its existence counts as a fourth criterion. Thus Wade (1979) and Bell (1978) hold that certain population structures are conducive to group selection. Some population structure variables vary continuously, such as the ratio of the variance of a trait within a sub-group to between sub-groups. There is a continuum of processes on which pure individual selection (with all the variance between individuals) and pure group selection (with all the variance between sub-groups) are the end-points. This criterion leads to their denial of any non-arbitrary and precise distinction between individual and group selection. The issue of individual-versus-group selection is a pseudo-problem and the real question is how population structure affects evolution. Their criterion likewise fails. For we already knew that heritable variation in fitness is a necessary but not sufficient criterion of selection at a given level from Williams' points about incidental effects. Heritable variation in fitness at one level plus selection for higher heritable fitness at that level may result in the fortuitous effect of heritable variation in fitness at some other level. Differential proliferation or extinction at the second level then arises solely from selection at the first level plus these relations. Thus, in the case of "pure group selection" with all the variance in fitness between groups and none within groups, selection between groups may arise as an incidental effect of selection between individuals. None of the proposed criteria deliver both necessary and sufficient conditions for selection at the group level, and in that sense fail as criteria.

Kuhn taught us that over-arching theoretical frameworks are afloat in a sea of anomalies from the very beginning which eventually inspire the overthrow of the old framework and allegiance to a new one. That point is well-illustrated by the units debate, which even preceded the evolutionary synthesis. These anomalies need not be merely empirical problems but often include conceptual problems. We can hardly begin to decide how important group selection is in historical evolution when we cannot even decide what makes the crucial difference between individual and group selection. So far criteria suggested by logically possible ways of departing from the DIS model have fallen short. Whether the units debate will eventually turn the anomalies victoriously into successful applications of the old framework properly understood or else yield counter-examples inspiring its demise is not yet known.

In using Kuhn's ideas of framework-articulation and anomalies, I do not mean to endorse his other ideas, e.g., relativism. I would guess that the relation between the old framework and that yet to come will not be one of "incommensurability", "theory-replacement", or "theory-reduction" in any extreme sense. Our discussion of criteria suggests that the new one will more likely be an "expansion" of the old one; it will take into account factors involving intricate relations between levels in its characterization of selection mechanisms, factors and levels on which the Darwinian pole of the synthesis was silent.

The units debate is possible because adherence to the synthetic framework advises us to follow methodological maxims which tell us what to do given the large number of logically possible ways to deviate from the DIS model and the felt need to do so. One maxim is to deviate from
the DIS model so as to explain traits within its scope in ways minimizing damage to the claim that all or most selection is individual selection. That maxim concerns the Darwinian pole and is essentially conservative, advising us to stick closely to what has worked in the past. Ontologically, it tells us to conceive selection mechanisms deviating from the DIS model as models of individual selection rather than group selection if possible and to maintain the assumption that the two processes are objectively distinct. Epistemologically, it tells us to accept group selection explanations only when efforts at explanation by individual selection are exhausted.

The maxim's presence explains much about the debate. It explains why ardent group-selectionists form an "out-group" in the sociological sense. It explains why Williams' proposal that we always try to explain adaptation at the lowest levels (e.g., the individual rather than the group) was so well accepted. It explains why our mere ability to invent plausible stories for how apparent cases of group selection could be cases of individual selection convinced naturalists to disregard group selection theories. And it explains why evolutionists retain the view that group selection cannot override the effects of individual selection except within a highly restricted set of parameter values, making group selection uncommon and unimportant in evolutionary history, despite proof to the contrary (Wade, 1978). In general, it explains why the burden of proof has always been awarded to the group selectionists.

A second maxim is to incorporate a genetic perspective into selection mechanisms. That maxim concerns the Mendelian pole of the synthesis. Its presence explains other distinctive features of the debate. It explains why the distinction between selfishness/altruism of the genotype and of the phenotype was made and considered central. It thereby explains the proliferation of theories made possible by that distinction and the associated presupposition that the unit of selection is a genetic unit. It also explains why kin selection was so enthusiastically received. Given an evolutionary genetic outlook, the organism's end is to perpetuate its gene-kinds, and which body they happen to be carried in is a subsidiary matter. Thus it was thought that an organism's own offspring are relevant to its fitness for the same reason that the offspring of relatives are relevant to its fitness: they share some proportion of its gene-kinds.

Searching criticisms of Dawkins doctrine of "the selfish gene" (Dawkins, 1976) have not done justice to its presuppositions. Given this synthesis-induced maxia, Dawkins takes a unit of selection to be a unit of benefit, a teleological unit, and a genetic unit. Dawkins (1984, 125) writes of the unit of benefit:

Adaptations are often spoken of as "for the good of" some entity, but what is that entity? Groups and species are now rightly unfashionable, so what are we left with? The prevailing answer is Darwin's "the individual". Individuals clearly do not maximize their own survival, so the concept of inclusive fitness had to be invented. If fitness is correctly defined in Hamilton's way as "inclusive fitness", it ceases to matter whether we speak of individuals as maximizing their inclusive fitness or of genes maximizing their survival. The two formulations are mutually inter-translatable.
If the two formulations were mathematically intertranslatable, the difference might matter philosophically, since mathematical intertranslatability does not guarantee ontological equivalence. Indeed, Dawkins' views are often attacked because they tend to make us affirm the gene's status and deny the organism's status as the basic entity of ontological significance in evolution. O'Donald (1982) has shown that inclusive fitness, what organisms subject to kin selection "strive" to maximize, is not even mathematically equivalent to genotypic fitness in population genetic models. The reason is that inclusive fitness is necessarily frequency-dependent, whereas the fitness of genotypes or phenotypes need not be. Further, to the extent that not all selection is kin selection, talk of inclusive fitness yields an incomplete view of selection's ontology.

Dawkins (1982, 45) writes with respect to the teleological unit:

The theory of natural selection provides a mechanistic, causal account of how living things come to look as if they had been designed for a purpose. So overwhelming is the appearance of purposeful design that, even in this Darwinian era when we know 'better', we still find it difficult, indeed boringly pedantic, to refrain from teleological language when discussing adaptation. Birds' wings are obviously 'for' flying, spider webs are for catching insects, chlorophyll molecules are for photosynthesis, DNA molecules for... What are DNA molecules for? The question takes us aback. In my case it touches off an almost audible alarm siren in the mind. If we accept the view of life that I wish to espouse, it is the forbidden question. DNA is not 'for' anything. If we wish to speak teleologically, all adaptations are for the preservation of DNA; DNA itself just is.

Speaking teleologically, an evolutionary ontology in which organisms were the basic existents might describe DNA molecules as 'for' the reproduction of organisms. Organisms use genes as the means to make more organisms. Dawkins reverses this to describe genes (germ-line replicators) as using organisms (survival machines or vehicles of genes) to perpetuate themselves. How are these opposing ontologies possible? Upon incorporating a genetic viewpoint into an appropriately expanded Darwinian scheme we have non-vicious circular causation: selection is a process in which differential survival/reproduction of objects at various levels of organization cause the differential perpetuation of genes causing those traits in virtue of which the differential survival/reproduction occurs.

The legitimacy of teleological talk in biology is under continual scrutiny. Three objections are especially relevant here. First, if selection is a causal non-teleological mechanism then talk of living things as being designed "for a purpose" is only a handy pedagogic metaphor and literally false. Second, selection operates the same way on organisms like spiders which have no purposes and on organisms like humans which do, making talk of organismic "purposes" usually false. Third, actions resulting in benefit to one's self-interest (a causal concept) are not selfish (a teleological concept) when they are not undertaken for that purpose, making it illegitimate to speak of selfishness/altruism rather than merely of self-interest/other-interest.
One initially plausible way out of Dawkins' schizoid position without becoming "boringly pedantic" is to bite the bullet of the first objection. To be justified in ascribing ends to organisms in the context of selection is to hold that selection is itself a teleological mechanism. The minimal sense in which this is true is that a trait is selected "for the sake of" its beneficial consequences to self or to others. Once we interpret a unit of benefit to be that which a trait is selected for in this sense, we have a view of selection which is both causal and teleological. To rebut the second objection we postulate that organisms do literally have ends, though not necessarily conscious motives or purposes. They have ends because they were created in part by a teleological mechanism. Their ultimate end is to fulfill the criterion of the selection mechanism. That criterion is fitness. From a genetic perspective the ultimate end of each organism is to maximize its genetic contribution to the gene pool of its evolving population in subsequent generations. To rebut the third objection we hold that selfishness rather than mere self-interest is involved in the sense that selfishness but not self-interest presumes a conflict between the interests of self and the interests of others. This conflict is insured by that fact that organisms are in reproductive competition according to selection theory. Since the ends of organisms (and objects at other levels according to the expanded selection theory) are always in conflict as reflected in the concept of relative fitness, organisms (and objects at other levels) are literally selfish in this minimal sense.

Despite Dawkins' denial that traits are for the good of groups, species, or individuals and affirmation that they are good for genes, he is now adamant about not trying to replace group or individual selection with genic selection. He contends that the levels of selection problem is different in kind from the units of selection problem. Whereas the levels problem concerns factual dispute about the level at which selection operates, the units problem concerns non-empirical considerations about what we ought to mean when we talk about a unit of selection. This position raises questions about the difference between empirical and non-empirical definitions which Dawkins has yet to answer. Those questions aside, we can use the concept of a unit of benefit to show an important sense in which the two problems are the same in kind on Dawkin's position. He claims that all selection is genic selection, i.e., that the unit of selection is always the gene no matter which level(s) selection operates on. To expand this claim, the levels problem concerns whether individuals or groups are the vehicles of genes which adaptations "are good for", and since some vehicles at a level are better than others at that level for ensuring the survival of their replicators, some vehicles are better at being "for the good of" their replicators than others. Here we have two uses of the concept of a unit of benefit.

Let us distinguish a "proximate" from an "ultimate" unit of benefit. When we think of what level adaptations are good for and selected on that basis we are thinking of the proximate unit of benefit. This concept links properties to objects: adaptive traits are good for objects at a certain level. When we think of what objects are units whose interests are benefited on an evolutionary time scale we are thinking of the ultimate unit of benefit. This concept links those objects to other objects: objects at any level are for the good of DNA. Dawkins (1982a, 86) defines the unit of selection as the "optimon", namely "the entity for whose benefit adaptations may be said to exist".
Dawkins' definition of the optimon can be criticized on the basis that genes are not objects which survive on an evolutionary time scale. Just as an organism's genotype and phenotype disappear when it does, so do its particular genes and traits. Only gene-kinds and trait-kinds have long-term survival. Even though genes are inherited from parents by offspring, the gene transmitted from those offspring to their offspring are different genes from those originally inherited. Token genes, i.e., particular physical objects, are not potentially immortal. Dawkins' notion of a replicator confuses tokens and types. What is transmitted is a copy of a token gene which is similar enough to the token gene to be a different token of the same type. The only object which is numerically one and the same and endures on an evolutionary time scale is the evolving population.

This criticism, due to Sober (1984, 251-52), can be rebutted by saying that the germ-line replicator endures as one and the same particular physical object without violating the type-token distinction. It is defined so that it exists in the form of copies of itself. These different copies are not different tokens but different stages in the existence of the very same object. That it makes sense to regard different replicators as different tokens of the same type, as when the type is defined by the common property of coding for a certain amino acid sequence, shows that the replicator concept does not confuse types with tokens. The reason I have chosen to say that traits are selected for the sake of their effects on gene-kinds rather than gene-instances (i.e., types rather than tokens) is that some selection mechanisms do not require that the donor and recipient of a phenotypically altruistic act share genes identical by descent (different copies of the same replicator inherited from a common ancestor). They only require that the donor and recipient share the same type of gene, e.g., the recipient's gene is newly mutated but has the same phenotypic function as the donor's gene.

3. THE DEBATE'S PHILOSOPHICAL STATUS AND POSSIBILITY

The units problem gains its philosophical status in virtue of its position as a foundational problem in biology. The preceding discussion suggests that it stands on its own merits as a philosophical problem because it connects interestingly to philosophical issues involving scientific theories. Among these are theory-choice, reductionism, relations between theories, scientific development, the conceptual structure of theories, and the ontology of theories. What bearing does the philosophical status of the problem have on the very possibility of the debate? These issues arise from the need, once evolutionary biology outgrew the identification of all selection with the DIS model, to find the best way of conceiving what makes something a unit of selection against the background of intricate relations between biological levels of organization.

Even though this answer is fundamentally sound, it is not complete. A complete answer would show how various presuppositions about what makes something a unit of selection are possible. To the extent that these presuppositions change yesterday's complete answer will not be complete today. Our discussion of the views held by E.O. Wilson, Ruse, and Dawkins emphasized three presuppositions held in common, or at least suggested beneath the surface of what they say. They take it to be a teleological unit, a unit of benefit, and a genetic unit. The recent book by Sober (1984), the best extended philosophical treatment of
the subject to date, turns these presuppositions on their head. Sober takes it to be a causal unit, a unit of possession, and not necessarily a genetic unit. Let us, then, clarify this clash of presuppositions.

Sober's main point is that the units problem has been confused by excessive concern with the concept 'selection of objects' and lack of attention to the concept 'selection of properties'. He writes (1984, 279) in this regard:

The first step toward clarification is to bring the idea of selection for properties to center stage. Group selection means that group properties cause differential survival and reproductive success. Genic selection means that genic properties are causally efficacious in this way. But this first step is not enough. It remains to be said what the objects are that these causally efficacious properties attach to. Organisms have genic properties, but so do chromosomes. Organisms belong to groups having certain group properties, but groups themselves also possess group properties.

Sober is not reticent in taking the unit of selection to be a causal unit; his book is about the role of causality in evolutionary theory. Notice that the causal construal leads him to take the unit of selection to be a unit of possession, i.e., "What the objects are that these causally efficacious properties attach to". The causal construal also leads him to deny that the unit of selection is always a genetic unit, for it may possess either phenotypic or genotypic ("genic") causally efficacious properties. Sober's three presuppositions exhibit an integrity equalling that of the Wilson-Ruse-Dawkins view. It should not require further argument to see that one cannot mix and match the three sets of opposing presuppositions at will and have a coherent position.

Sober turns his point of clarification into two definitions (1984, 280):

So the idea is that there is group selection for groups that have some property P if (and only if)

1. Groups vary with respect to whether they have P, and
2. There is some common causal influence on those groups that makes it the case that
3. Being in a group that has P is a positive causal factor in the survival and reproduction of organisms.

The analysis of genic selection goes in parallel. There is selection for possessing the gene P if (and only if)

1. Organisms vary with respect to whether they have P, and
2. There is some common causal influence on those organisms that make it the case that
3. Possessing the gene P is a positive causal factor in the survival and reproduction of organisms.
Even though clause (3) in each definition refers to organisms as the objects benefiting from selection, Sober holds that if it were modified to speak of reproductive benefits at some other level that difference would not change the unit of selection. He holds this because he takes the unit of benefit to be irrelevant to question of what counts as a unit of selection. However, it is not clear what counts as the unit of possession in these definitions, due to an obvious disparity. In the definition of group selection groups possess the causally efficacious property. But in the definition of genic selection genes don't appear to possess the property. Rather, organisms possess it. So if we take clause (1) in each definition to yield the unit of selection, the first definition is of group selection and the second of individual selection. But if we take the left side of each biconditional to yield the unit of selection, the first definition is of group selection and the second of genic selection. Suppose we were to change the property in the second definition from 'possessing gene P' to 'being a member of a group with property P'. Then the second definition would be of group selection according to the left side of its modified biconditional, yielding two different definitions of group selection.

Prior to cleaning up the definitions so as to avoid this confusing result, it seems that Sober has not defined "selection at a level" at all. He has defined "selection for having the property P", namely, that having P is selected for because possessing it causes reproductive success. But who possesses P? He fails to clarify how the concept of selection for properties is to hook up with the concept of objects having the property selected for. Yet to leave it at this would be unsympathetic to Sober's definitions. They reflect facts about inter-level relations which cannot be ignored, namely that organisms and genes possess genic properties or that organisms and groups possess group properties.

Just as Dawkins' views were clarified by distinguishing "the ultimate unit of benefit" from the "proximate unit of benefit", a similar distinction is appropriate here. In each definition clause (1) specifies a "proximate property" and a "proximate unit of possession". In the first definition P is the proximate property and it is possessed by groups, which form the proximate unit of possession. In the second definition P is the proximate property and it is possessed by organisms, which form the proximate unit of possession. In each definition clause (3) specifies an "ultimate property" and an "ultimate unit of possession". In the first definition 'being in a group that has P' is the ultimate property and organisms form the ultimate unit of possession. In the second definition 'possessing the gene P' is the ultimate property and organisms again are the ultimate unit of possession. A "trait unit of possession" is an object mentioned in either the description of a proximate or ultimate property. In the second definition the genes mentioned in the ultimate property's description is the trait unit of possession. Thus, we have expanded our linguistic resources to take account of inter-level relations and avoid the previous confusion by stating which sense of a "unit of possession" is utilized. Some selection mechanisms are comprehensible without these distinctions, but those incorporating inter-level relations may require them.

It should be emphasized that we cannot answer our question of what makes the debate possible by saying that different levels may be considered as units of selection in the sense of Wilson-Dawkins-Ruse.
Their presuppositions as well as Sober's are part of the debate and do not make it possible. To show how the opposing presuppositions are themselves possible we should return to the DIS model and exhibit it as a special case of a more abstract structure. The debate is possible—in its full sense of including opposing presuppositions—because different decisions can be made about how to best interpret this abstract structure as needed to transcend the DIS model.

Let us abstract the DIS model away from explicit commitment to organisms being the unit of selection without unnecessary formalization. The abstract structure describes two kinds of objects. Objects of kind P form the unit of possession, as they possess traits conferring differential heritable fitnesses on objects of kind B. Objects of kind B form the unit of benefit, as they benefit differentially from traits possessed by objects of kind P. The units of possession and benefit are thus described through inter-defined concepts, though the two concepts are different. We shall omit reference to results of the mechanism which are not strictly part of the mechanism itself and occur in conditions not specified by the DIS model: the maximization of average fitness and speciation.

(1) Principle of competition: Objects of kind B are capable of reproducing more of their number than will survive. (2) Principle of inherited variation in fitness: Some objects of kind P have traits which confer on objects of kind B higher heritable fitnesses than other objects of kind B are given in virtue of the traits of other objects of kind P. (3) Principle of greater reproductive survival of objects: Objects of kind B with higher heritable fitnesses survive to reproduce more often, on the average, than objects of kind B with lower heritable fitnesses in proportion to their differential fitness. (4) Principle of greater representation of traits: Heritable traits of objects of kind B with higher fitnesses are represented at a greater frequency, on the average, in the population in the next generation than heritable traits of objects of kind B with lower fitnesses in proportion to their differential fitness.

The selection mechanism of the concrete DIS model is a special case of that described in this abstract model on the following suppositions. (1) cites the source of reproductive competition in environment-related density-dependent mortality. This shows that selection mechanisms are possible in which mortality is density-independent and not necessarily environment-related. (1)-(5) require that objects of kind P and objects of kind B are identical organisms. This shows that selection mechanisms are possible in which the units of possession or benefit are non-identical organisms, identical but not organisms, or non-identical and not organisms. (2) and (4) require that the traits of objects of kind P conferring higher heritable fitnesses are the same as the heritable traits of objects of kind B increasing in frequency. This shows that selection mechanisms are possible in which the traits selected for are different from the traits increasing in frequency.

As cited in earlier proposed criteria for distinguishing individual from group selection, further selection mechanisms are possible by describing what sorts of traits are involved, relations between objects at the same or different levels constituting the units of possession and benefit, relations between the fitnesses and traits of these objects, and various sorts of population structure. As suggested by the previous clarifications of Dawkin's and Soter's position, still further selection
mechanisms are possible which distinguish different senses of the unit of possession concept or the unit of benefit concept or both. Of course, such mechanisms deviating from the concrete DIS model in these ways require the right mathematical formulation to make them work and will not be fully described as special cases of this abstract structure. One might use these distinctions to classify possible selection mechanisms in the hope of helping theoretical biology recognize unforeseen possibilities.

Recourse to this abstract structure clarifies the relation between the units and the levels of selection. Wimsatt (1984, 163) defines a "unit of selection" in terms of levels. Brandon (1982, 315) claims that the units issue is different from the levels issue. He takes Wimsatt's definition as relevant to the units issue, and offers a definition of "selection at a level" designed to express the idea that the causal process of selection operates directly on objects at that level. We have seen that Sober defines group and genic selection but did not explicitly state the connection between the units and the levels issue. Our abstract structure shows that selection mechanisms are describable without essential reference to levels. Why not state the broad lines of the causal approach as follows, using group selection to illustrate selection at a level? Group selection occurs if and only if there is selection at the group level. Selection at a level occurs if and only if objects at that level form a unit of selection. Objects at a given level are always objects of a certain kind, for levels are merely an ordering relation among objects of various kinds, a relation involving spatial or temporal scale. Objects of a certain kind form a unit of selection if and only if the causal mechanism of selection operates appropriately on them. The causal mechanism operates appropriately on objects of a certain kind if and only if those objects form a unit of possession, i.e., they possess traits causing differential fitness.

Second, recourse to the abstract structure clarifies the issue over whether the unit of selection need be a genetic unit. Sober's definitions have selection requiring variation in traits but no heritable variation in fitness. His definitions are offered as defining a unit of selection. Selection without evolution occurs when heritability is absent. His definitions are at cross-purposes with those of most evolutionists, whose lack of interest in selection except insofar as it produces evolutionary change makes heritability necessary, and are thinking of a unit of evolution by selection. Given their different purposes, each side is right. In (2) of the abstract model we see that heritability relates to the unit of benefit but not to the unit of possession. Since Sober is taking the causal approach and thinking of the unit of selection as the unit of possession, he is right to regard heritability as irrelevant. Since Dawkins is taking the teleological approach and thinking of the unit of selection as the unit of benefit, he is right to regard heritability as required. Once heritability is regarded as required, could we regard genetic causation of traits as merely a way of insuring heritability and not part of the selection mechanism? If so, we would be driven to conceiving the process in which some supernatural being like God insures that fitnesses of offspring are positively correlated with parental fitnesses as natural selection, even though our intuitions tell us that it would be supernatural selection. Further, if we accept the units problem as occurring within the framework of the synthesis, accepting the maxim to reinterpret selection genetically, our commitment compels us to take the unit of selection to be a genetic unit.
Third, recourse to the abstract structure clarifies the relation between the teleological and causal views of the unit of selection. It is unsympathetic to evolutionists for Sober (1984, 278-81) to suggest that they have only considered what a unit of selection is in terms of what objects are selected and have ignored selection for properties. It is common knowledge that DIS involves selection for advantageous variations and that these variations are properties. Our abstract model makes this explicit. It distinguishes objects, kinds of objects, traits, and fitnesses. It distinguishes greater reproductive survival of objects from greater representations of traits. Whereas the causal theorist focuses on objects forming the unit of possession and their properties, the teleological theorist focuses on objects forming the unit of benefit and their properties. Both parties have assimilated Sober's distinction between selection for properties and selection of objects from reading Williams (1966) rebuttal to naive group selectionists. Williams argued that most or all cases of apparent group selection were cases of individual selection even though organismic properties fortuitously benefit groups. In such cases there is selection of groups without selection for those organismic properties.

The reason for mis-communication is readily reconstructed. Williams shows that the appearance of group selection is given by an incidental effect of individual selection. Therefore, thinking merely in terms of who benefits from selection does not pinpoint the level at which it operates and leaves open the question of what counts as a unit of selection. The concept of selection for properties records the causes of evolution by selection, whereas the concept of selection of objects records the effects of evolution by selection and is only suitable for "bookkeeping". In this way Sober is motivated to identify the unit of selection with a causal unit and a unit of possession.

Sober too quickly dismisses the views of Dawkins and other teleologists, who do not identify the unit of benefit with whoever happens to benefit from selection. For we want to distinguish, as did Ruse, between incidental and nonincidental effects or benefits. By hypothesis, here the benefit to the group is incidental. The unit of benefit is not the group because group selection requires that the beneficial effect is not incidental, which means that the benefit occurs as part of the selection mechanism itself. Incidental beneficial or costly effects occur in virtue of a certain relation. That is the relation between objects/properties in the historical selective situation, including other sources of change like genetic drift and migration, and at least one selection mechanism operative in that situation. The teleologist must not be denied the conceptual resources to make his case, which includes discrimination between incidental and end-oriented effects. The teleologist requires that the unit of benefit be that for the sake of which the selected trait is selected, a condition unfulfilled in the cases of naive group selectionist explanations criticized by Williams.

Sober (1984, 313) argues that Dawkin's position (i.e., all selection is genic selection) will not hold for normal cases of genes affecting many traits:

The problem is polygenic effects. If a gene raises the probability of a given phenotype in one context and lowers it in
another, there is no such thing as the causal role that the gene has in general. Selection for or against the phenotype may cause the frequency of the gene to change, but this will be due to the correlation between gene and phenotype. There will be selection of the gene, but no selection for it.

Sober's conclusion is that genic selectionism has only minimal scope because it fails to apply to cases in which single genes have no general causal role, that role being possessed by ensembles of genes or higher-level objects. But this argument presupposes that the unit of selection is a causal unit and a unit of possession, which begs the question against Dawkins. Dawkins does not require that single genes have a general causal role, only that traits selected are selected for the sake of their effect on heritable variations in fitness, on the perpetuation of the genes of some object. When the unit of possession is not identical to the unit of benefit, the genes of the unit of benefit to be perpetuated need not have any causal role on the production of the trait had by the unit of possession, much less a uniform context-independent role.

Sober's argument from polygenic effects associates causation with the concept of 'selection for' and associates correlation with the concept of 'selection of'. But both the causal and teleological approaches are conceptually richer and more restrictive concepts than that of mere correlation. When an operative selection mechanism selects for traits of objects of kind P for the sake of their effect on the reproductive survival of objects of kind B, and the differential survival of objects of kind B is positively correlated with that of objects of kind E, then there is selection of objects of kind E. We may call the objects of kind E a "unit of effect". Although the concept of selection of objects merely expresses correlation, the unit of benefit concept is obviously here not the same as the unit of effect concept. So Sober's argument misses the teleological theorist's point entirely.

Correlation is a symmetric relation which fails to support counterfactuals. Both causation and means-end relations are asymmetric, support counterfactuals, and concern selection for properties. The selection of objects of kind E having trait T neither implies the selection for objects of kind E having T nor, by that very fact, the selection for objects of kind E having T for the sake of their having T. But the selection for objects of kind E having T for the sake of their (or some other unit of benefit's) having T trivially implies the selection for objects of kind E having T. The teleological approach implies the truth of the causal approach and goes beyond it. It is false that there is selection of objects of kind E even if those objects had not differentially survived to reproduce. But it may be true that there is selection for properties of objects of kind P and that those properties are selected for the sake of their effect on the reproductive survival of objects of kind B, even if as a matter of fact favored objects of kind B do not better survive to reproduce, e.g., due to to such interfering factors as genetic drift or countering selection in the actual historical selective situation.

What makes the unit debate possible is that any abstractly formulated selection mechanism admits to both a causal and a teleological interpretation. Both interpretations are needed to handle cases of apparent but not genuine selection at some level, cases motivating the distinction between what happens as part of a selection mechanism and
what happens due to its relation to the actual, historical situation. A pure causal approach specifies what kind of unit of possession is but leaves what kind the unit of benefit is unspecified. To generalize Sober's definitions, objects of kind P form a unit of selection if and only if they vary with respect to whether they possess trait T and there is a common causal influence on them which makes T a positive causal factor in the reproductive survival of objects of kind B, no matter what kind B is. A pure teleological approach specifies what kind the unit of benefit is but leaves what kind the unit of possession is unspecified. Analogously, objects of kind B form a unit of selection if and only if they exhibit heritable variation in fitness and objects of kind P possess some trait T such that T is selected for the sake of its benefit to objects of kind B, no matter what kind P is.

I propose that we reject both the pure causal and pure teleological interpretations. Though no full blown justification of causal or of means-end talk in biological contexts has been attempted, the overall effect of our discussion is to suggest that both approaches are needed to make the discriminations we need to make in order to handle cases of apparent but not genuine selection at a level. Further, the concepts of a unit of possession and a unit of benefit are inter-definable on any model of a selection mechanism promoting the evolution of some trait. Each concept is defined relative to that trait. With respect to some advantageous trait T, the unit of possession is interpreted causally as that which possesses T such that its having T causes differential reproductive survival of some unit of benefit. With respect to T, the unit of benefit interpreted teleologically is that which is benefited by T such that the unit of possession's having T is selected for the sake of its beneficial effect to that which is benefited. These considerations suggest a new criterion for a unit of selection. Something is a unit of selection if and only if it is the pair consisting of a unit of possession and a unit of benefit defined in this way.

An immediate consequence is that it is misleading to frame our problem in terms of genic versus individual versus group selection. This is not merely because genes of individuals or of groups count as units of benefit in genetic models, but because the units of possession and benefit may be at different levels. In such cases we might mention the unit of possession first and the unit of benefit second, speaking of individual-group or group-individual selection. Such changes of language are needed now that we have outgrown the DIS model's identification of the objects forming the units of possession and benefit.

A virtue of this proposal is that it does justice to widely held presuppositions about what makes something a unit of selection. Also, it is not so closely linked to views that fit some selection model that they fail to fit others. I know of no other proposed criterion that is general enough to avoid putting unnecessary empirical restrictions on the sorts of selection models devised by theoretical biologists and still points out a common feature of all foreseeable models which has some conceptual "teeth" to it. In this spirit the most we can do is to say what objects form a unit of selection on some model by pointing out what objects form the pair of units on that model. Flexibility is enhanced by noting that some models are sufficiently complex to involve more than one unit of possession and more than one unit of benefit. One way to do this is to distinguish proximate and ultimate units of each or otherwise make
distinctions between various units of each sort, e.g., unit of phenotypic or genetic benefit.

In conclusion, I have sought to answer the much ignored question of what makes the units or levels of selection debate possible. I have argued that one plausible answer is couched in terms of logically possible ways to deviate from the DIS model, restrictions on those ways imposed by the evolutionary synthesis, and further restrictions imposed by the causal and teleological interpretations of the abstract structure of selection mechanisms. In developing this answer I have sought to provide a unified picture of the debate by emphasizing the clash of opposing basic presuppositions with the help of a distinction between the unit of possession and the unit of benefit. This effort has led not only to a more adequate understanding of the units or levels problem but also to a new way of conceiving what a unit of selection is. The new conception promises to do justice to both sets of basic presuppositions and to the intricate relations among biological levels of organization.

REFERENCES


