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Edited by

RAMA S. SINGH

McMaster University

COSTAS B. KRIMBAS

University of Athens

DIANE B. PAUL

University of Massachusetts at Boston

JOHN BEATTY

University of Minnesota

2001

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Notes

1. *The Dialectical Biologist* (1985) includes much work that Levins and Lewontin had published independently. They say that the essay "Dialectics" was cowritten especially for the collection, however.
2. When the adaptationist view is combined with atomism in this way, one of Lewontin's arguments against adaptationism can be fended off. Lewontin says that the adaptationist has a problem because the concept of a "niche" is predictively empty, for niches do not exist until organisms fill them (1985, p. 98). But a niche is a *total* way of life involving a whole package of traits. Thus, an atomist, who treats each trait of an organism separately, does not have to predict or explain which total lifestyle possibilities will be found in nature – which niches will be filled.

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CHAPTER THIRTEEN

Units and Levels of Selection

An Anatomy of the Units of Selection Debates

ELISABETH A. LLOYD

13.1 Introduction

Richard Lewontin was the first to investigate systematically the set of problems raised by a hierarchical expansion of selection theory in his landmark 1970 article. His classic abstraction and analysis of the three principles of evolution by natural selection – phenotypic variation, differential fitness, and heritability of fitness – have served as the launching point for many biologists and philosophers who have wrestled with units of selection problems. Lewontin's critical discussion of the empirical evidence for selection at various biological levels has served as both touchstone and target for later work. But Lewontin's essay was addressed to the efficacy of different units of selection as causes of evolutionary change (1970, p. 7). In the analysis I offer in this chapter, this is but one of four distinct questions involved in the contemporary units of selection debates.

For at least two decades, some participants in the "units of selection" debates have argued that more than one question is at stake. Richard Dawkins, for instance, introduced the terms *replicator* and *vehicle* to stand for different roles in the evolutionary process (1978; 1982a,b). He proceeded to argue that the units of selection debate should not be about vehicles, as it had formerly been, but about replicators. David Hull, in his influential article, "Individuality and Selection" (1980), suggested that Dawkins' "replicator" subsumes two distinct functional roles, and the separate categories of "replicator," "interactor," and "evolver" were born. Brandon, arguing that the force of Hull's distinction had not been appreciated, analyzed the units of selection controversies further, claiming that the question about interactors should more accurately be called the "levels of selection" debate to distinguish it by name from the dispute about replicators, which he allowed to keep the "units of selection" title (1982).¹

This analysis was first presented in July 1989 at the Plenary session of the International Society for the History, Philosophy, and Social Studies of Biology. In November 1989, it was delivered to the Genetics Colloquium at Harvard and distributed to the NSF Workshop on Development and Evolution, at the Santa Fe Institute.

My purpose in this chapter is to delineate further the various questions pursued by Robert Brandon, Richard Dawkins, James Griesemer, David Hull, Richard Lewontin, John Maynard Smith, Sandra Mitchell, Elliott Sober, Michael Wade, George C. Williams, David S. Wilson, William Wimsatt, Sewall Wright, and many others under the rubric of "units of selection."² I will isolate four quite distinct questions that have, in fact, been asked in the context of considering, What is a unit of selection? In Section 13.2, I describe each of these distinct questions. In Section 13.3, I return to the sites of several very confusing, occasionally heated debates about "the" units of selection. I analyze many leading positions on the issues using my taxonomy of questions.

This analysis does not, of course, make differences vanish, but I hope to clarify the terms of the debates. My analysis also does not resolve any of the conflicts about which research questions are most worth pursuing; moreover, I do not attempt to decide which of the questions or combinations of questions I discuss ought to be considered *the* units of selection question. Although I have elsewhere argued that the interactor question (see Section 13.2.1) is a primary question for evolutionary genetics, that claim is intended as historical and descriptive; most evolutionary genetics models that address any version of the units of selection question have focused on which level of interaction must be represented in the model to make it dynamically and empirically adequate (Lloyd 1988, especially Chapters 5 and 6).³ Furthermore, the mere persistence of the three other questions to be discussed attests to their importance and general interest.

13.2 Four Basic Questions

Four basic questions can be delineated as distinct and separable. As we shall see in Section 13.3, these questions are often used in combination to represent *the* units of selection problem. But before we continue, we need to clarify some terms.

The term *replicator*, originally introduced by Dawkins but since modified by Hull, is used to refer to any entity of which copies are made. Dawkins classifies replicators using two orthogonal distinctions. A "germ-line" replicator, as distinct from a "dead-end" replicator, is "the potential ancestor of an indefinitely long line of descendant replicators" (1982a, p. 46). For instance, DNA in a chicken's egg is a germ-line replicator, whereas that in a chicken's liver is a dead-end replicator. An "active" replicator is "a replicator that has some causal influence on its own probability of being propagated," whereas a "passive" replicator is never transcribed and has no phenotypic expression whatsoever (1982a, p. 47). Dawkins is especially interested in *active germ-line replicators*, "since adaptations 'for' their preservation are expected to fill the world and to characterize living organisms" (1982a, p. 47).

Dawkins also introduced the term *vehicle*, which he defines as "any relatively discrete entity . . . which houses replicators, and which can be regarded as a machine programmed to preserve and propagate the replicators that ride inside

it" (1982b, p. 295). According to Dawkins, most replicators' phenotypic effects are represented in vehicles, which are themselves the proximate targets of natural selection (1982a, p. 62).

Hull, in his introduction of the term *interactor*, observes that Dawkins' theory has replicators interacting with their environments in two distinct ways: they produce copies of themselves, *and* they influence their own survival and the survival of their copies through the production of secondary products that ultimately have phenotypic expression. Hull suggests the term *interactor* for entities that function in this second process. An *interactor* denotes that entity which interacts, as a cohesive whole, directly with its environment in such a way that replication is differential – in other words, an entity on which selection acts directly (Hull 1980, p. 318). The process of evolution by natural selection is "a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them" (Hull 1980, p. 318; cf. Brandon 1982, pp. 317–8).

Hull also introduced the concept of "evolvers," which are the entities that evolve as a result of selection on interactors; these are usually what Hull calls "lineages" (Hull 1980). So far, no one has directly claimed that evolvers are units of selection. They can be seen, however, to be playing a role in considering the questions of who owns an adaptation and who benefits from evolution by selection, which we will consider in Section 13.3.1 and 13.3.3.

13.2.1 The Interactor Question

In its traditional guise, the interactor question is, What units are being actively selected in a process of natural selection? As such, this question is involved in the oldest forms of the units of selection debates (Darwin 1859 (1964), Haldane 1932, Wright 1945). In his classic review article, Lewontin's purpose was "to contrast the levels of selection, especially as regards their efficiency as causes of evolutionary change" (1970, p. 7). Similarly, Slobodkin and Rapaport assumed that a unit of selection is something that "responds to selective forces as a unit – whether or not this corresponds to a spatially localized deme, family, or population" (1974, p. 184).

Questions about interactors focus on the description of the selection process itself, that is, on the interaction between entity and environment and on how this interaction produces evolution; they do not focus on the outcome of this process (see Wade 1977, Vrba and Gould 1986). The interaction between some interactor and its environment is assumed to be mediated by "traits" that affect the interactor's expected survival and reproductive success. (N.B. – An interactor may be at any level of biological organization, including a group, an organism, a chromosome, a kin group, or a gene.) In other words, some portion of the expected fitness of the interactor is directly correlated with the "value" of the trait in question. The expected fitness of the interactor is commonly expressed in terms of genotypic fitness parameters, that is, in terms of the fitness of combinations of replicators; hence, interactor success is most often reflected

in, and counted through, replicator success. Several methods are available for expressing such a correlation between trait and (genotypic or organismic) fitness, including regression and variances, and covariances. Several models are also available for representing interactors; in all of these, the interactor's trait is correlated with replicator fitness values, and the component of the replicator fitnesses attributed to the interactor is not available or reproducible from a lower level of interactor.⁴

In fact, much of the interactor debate has been played out through the construction of mathematical genetical models. The point of building such models is to determine what kinds of selection, operating on which levels, may be effective in producing evolutionary change.

It is widely held, for instance, that the conditions under which group selection can effect evolutionary change are quite stringent and rare. Typically, group selection is seen to require small group size, low migration rate, and extinction of entire demes.⁵ Some modelers, however, disagree that these stringent conditions are necessary. Matessi and Jayakar, for example, show that in the evolution of altruism by group selection, very small groups may not be necessary (1976, p. 384; contra Maynard Smith 1964); Wade and McCauley also argue that small effective deme size is not a necessary prerequisite to the operation of group selection (1980, p. 811). Similarly, Boorman shows that strong extinction pressure on demes is not necessary (1978a, p. 1909). And finally, Uyenoyama develops a group selection model that violates all three of the "necessary" conditions usually cited (1979).

That different researchers reach such disparate conclusions about the efficacy of group selection is partly because they are using different models with different parameter values. Wade highlighted several assumptions, routinely used in group selection models, that biased the results of these models against the efficacy of group selection (1978). For example, he noted that many group selection models use a specific mechanism of migration; it is assumed that the migrating individuals mix completely, forming a "migrant pool" from which migrants are assigned to populations randomly. All populations are assumed to contribute migrants to a common pool from which colonists are drawn at random. Under this approach, which is used in all models of group selection prior to 1978, small sample size is needed to get a large genetic variance between populations (Wade 1978, p. 110).

If, in contrast, migration occurs by means of large propagules, higher heritability of traits and a more representative sampling of the parent population will result. Each propagule is made up of individuals derived from a single population, and there is no mixing of colonists from different populations during propagule formation. On the basis of Slatkin and Wade's analysis, much more between-population genetic variance can be maintained with the propagule model (1978, p. 3531). They conclude that, by using propagule pools as the assumption about colonization, one can greatly expand the set of parameter values for which group selection can be effective (Slatkin and Wade 1978, p. 3531; cf. Craig 1982).

My point here is not, however, to survey the various models⁶ but rather to illustrate the *level of disagreements* within the interactor question itself. It should also be emphasized that not all discussion regarding which levels of selection are causally efficacious has been quantitative. Many authors have attempted to determine which levels of selection must or should be taken into account through qualitative descriptions of interactors.⁷

Note that what I am calling the "interactor question" does *not involve attributing adaptations or benefits to the interactors*. Interaction at a particular level involves only the presence of a trait at that level with a special relation to genic or genotypic expected success that is not decomposable into fitness components at another level.⁸ A claim about interaction indicates only that there is an evolutionarily significant interaction occurring at the level in question; it says nothing about the existence of adaptations at that level. As we will see, the most common error made in interpreting many of the genetical models is that the presence of an interactor at a level is taken to imply that the interactor is also a manifestor of an adaptation at that level.

13.2.2 Replicators

Starting from Dawkins' view, Hull refined and restricted the meaning of "replicator," which he defined as "an entity that passes on its structure directly in replication" (1980, p. 318). I will use the terms *replicator* and *interactor* in Hull's sense throughout the rest of this chapter.

Hull's definition of replicator corresponds more closely than Dawkins' to a long-standing debate in genetics about how large or small a fragment of a genome ought to count as the replicating unit – something that is copied, and which can be treated separately (see especially Lewontin 1970). This debate revolves critically around the issue of linkage disequilibrium and led Lewontin, most prominently, to advocate the usage of parameters referring to the entire genome rather than to allele and genotypic frequencies in genetical models.⁹

The basic point is that with much linkage disequilibrium, individual genes cannot be considered as replicators because they do not behave as separable units during reproduction. Although this debate remains pertinent to the choice of state space for genetical models, it has been eclipsed by concerns about interactors in evolutionary genetics.

13.2.3 Beneficiary

Who benefits from a process of evolution by selection? There are two predominant interpretations of this question: Who benefits ultimately, in the long term, from the evolution by selection process? and Who gets the benefit of possessing adaptations as a result of a selection process?

Take the first of these, the issue of the ultimate beneficiary. There are two obvious answers to this question – two different ways of characterizing the

long-term *survivors and beneficiaries* of the evolutionary process. One might say that the species or lineages (Hull's "evolvers") are the ultimate beneficiaries of the evolutionary process. Alternatively, one might say that the lineages characterized on the genic level, that is, the surviving alleles, are the relevant long-term beneficiaries. I have not located any authors holding the first view, but, for Dawkins, the latter interpretation is *the primary fact* about evolution. To arrive at this conclusion, Dawkins adds the requirement of *agency* (cf. Hampe and Morgan, 1988). For Dawkins, a *beneficiary*, by definition, does not simply passively accrue credit in the long term; it must function as the initiator or causal source of a biochemical causal pathway. Under this definition, the *replicator* is causally responsible for all of the various effects that arise further down the biochemical pathway, irrespective of which entities might reap the long-term rewards.¹⁰

A second and quite distinct version of the "benefit" question involves the notion of adaptation. The evolution by selection process may be said to "benefit" a particular level of entity under selection, though producing *adaptations* at that level (Williams 1966, Maynard Smith 1976, Eldredge 1985, Vrba 1984). On this approach, the level of entity actively selected (the interactor) *benefits* from evolution by selection at that level through its acquisition of adaptations.

I think it is crucial to distinguish the question concerning the level at which adaptations evolve from the question about the identity of the ultimate beneficiaries of that selection process. One can think – and Dawkins does – that organisms have adaptations without thinking that organisms are the "ultimate beneficiaries" of the selection process.¹¹ I will therefore treat this sense of "beneficiary" that concerns adaptations as a separate issue, discussed in the next section, under the topic of the manifestor of adaptations.

13.2.4 Manifestor of Adaptations

At what level do adaptations occur? Or, as Sober puts this question, "When a population evolves by natural selection, what, if anything, is the entity that does the adapting?" (1984, p. 204).

As mentioned previously, the presence of adaptations at a given level of entity is sometimes taken to be a *requirement* for something to be a unit of selection.¹² Wright, in an absolutely crucial observation, distinguished group selection for "group advantage" from group selection *per se* (1980); in my terms, he claimed that the combination of the interactor question with the question of what entity had adaptations had created a problem in the group selection debates. Following Wright, I submit that the identification of a unit of selection with the manifestor of an adaptation at that level has caused a great deal of confusion in the units of selection debates in general.

Some, if not most, of this confusion is a result of a very important but neglected duality in the meaning of "adaptation" (in spite of useful discussions in Brandon 1978b, Burian 1983, Krimbas 1984, Sober 1984). Sometimes "adaptation" is taken to signify *any trait at all* that is a direct result of a selection

process at that level. In this view, any trait that arises directly from a selection process is claimed to be, *by definition*, an adaptation (e.g., Sober 1984; Brandon 1985, 1990; Arnold and Fristrup 1982).¹³ Sometimes, on the other hand, the term "adaptation" is reserved for traits that are "good for" their owners, that is, those that provide a "better fit" with the environment, and that intuitively satisfy some notion of "good engineering."¹⁴ These two meanings, which I call the *selection-product* and *engineering* definitions, respectively, are distinct, and in some cases, incompatible.

Williams, in his extremely influential book, *Adaptation and Natural Selection*, advocated an engineering definition of adaptation (1966). He believed that it was possible to have evolutionary change result from direct selection favoring a trait *without* having to consider that changed trait as an *adaptation*. Consider, for example, his discussion of Waddington's (1956) genetic assimilation experiments. Williams interprets the results of Waddington's experiments in which latent genetic variability was made to express itself phenotypically because of an environmental pressure (1966, pp. 70–81; see the lucid discussion in Sober 1984, pp. 199–201). Williams considers the question of whether the bithorax condition (resulting from direct artificial selection on that trait) should be seen as an adaptive trait, and his answer is that it should not. Williams instead sees the bithorax condition as "a disruption . . . of development," a failure of the organism to respond (1966, pp. 75–8). Hence, Williams draws a wedge between the notion of a trait that is a direct *product* of a selection process and a trait that fits his stronger *engineering* definition of an adaptation (see Gould and Lewontin 1979; Sober 1984, p. 201; cf. Dobzhansky 1956).¹⁵

This essential distinction between the *selection-product* and *engineering* views of adaptation is far from widely recognized. My claim here is that greater awareness of this distinction and its consequences will contribute to the understanding of several very heated debates in evolutionary theory.

For example, the engineering notion of adaptation is at work in the long dispute over the relationship between natural and sexual selection. Many evolutionists, starting with Darwin, rejected the idea that the products of a sexual selection process should be considered *adaptations*. In fact, analysis of the process of sexual selection is sometimes motivated by the drive to find an explanation for the presence of "maladaptive" traits; hence, the distinction between the selection-product and engineering notion of adaptation plays an important role. Kirkpatrick (1987), for instance, uses a notion of adaptedness based on mean survival values in his argument that sexual selection does not always produce adaptations.

Consider for a moment the two schools of sexual selection theory. The "good genes" school claims that mate choice evolves under selection for females to mate with ecologically adaptive genotypes. The assumption here is that even though it appears that the females are basing their mate choice on a nonadaptive character, the character is actually an indication of the male's adaptedness (see, e.g., Vehrencamp and Bradbury 1984, Hamilton et al. 1990). The "nonadaptive" school claims that "preferences frequently cause male traits to

evolve in ways that are *not adaptive* with respect to their ecological environment" (Kirkpatrick 1987, p. 44; emphasis added). In other words, the kinds of males preferred by females do not correspond with the kinds of males favored by natural selection. The result is a compromise between natural and sexual selection, the final state being one "that is maladaptive with respect to what natural selection acting alone would produce" (Kirkpatrick 1987, p. 45). Sir Ronald Fisher developed mathematical models showing how preferences for maladaptive males could evolve (1958 [1930]; see discussion in Lande 1980; Spencer and Masters 1992; Cronin 1991).

But an alternate concept of adaptation is available: the sexually selected traits that are advantageous to mating can still be seen as adaptations once the meaning of "adaptation" is adjusted. In this school of thought, the notion of "adaptation" should be broadened to include traits that contribute exclusively to reproductive success even though the more traditional definition is in terms of engineering for survival (e.g., Cronin 1991 versus Bock 1980; see Kirkpatrick 1987).

As these perennial debates about the relation between sexual selection and natural selection show, when asking whether a given level of entity possesses adaptations, it is necessary to state not only the level of selection in question but also which notion of adaptation – either *selection-product* or *engineering* – is being used. This distinction between the two meanings of adaptation also turns out to be pivotal in the debates about the efficacy of higher levels of selection, as we will see in Sections 13.3.1 and 13.3.3.

13.2.5 Summary

In this section, I have described four distinct questions that appear under the rubric of "the units of selection" problem: What is the interactor? What is the replicator? What is the beneficiary? and What entity manifests any adaptations resulting from evolution by selection? I have also discussed the existence of a very serious ambiguity in the meaning of "adaptation." I have no intention of defending one meaning or the other, but I will show that *which* meaning is in play has had deep consequences for both the group selection debates and the species selection debates. In Section 13.3, I will use my taxonomy of questions to sort out the most influential positions in three debates: group selection (Section 13.3.1), genic selection (Section 13.3.2), and species selection (Section 13.3.3).

13.3 An Anatomy of the Debates

13.3.1 Group Selection

Williams' famous near-deathblow to group panselectionism was, oddly enough, about benefit. He was interested in cases in which there was selection among groups and the group as a whole *benefited from* organism-level traits (including behaviors) that seemed disadvantageous to the organism.¹⁶ Williams argued that the presence of a benefit to the group was *not sufficient* to establish the

presence of group selection. He did this by showing that a group benefit was not necessarily a group adaptation.¹⁷ His assumption was that a genuine group selection process results in the evolution of a group-level trait – a real adaptation – that serves a design purpose for the group. The mere existence, however, of traits that benefit the group is not enough to show that they are adaptations; in order to be an adaptation, under Williams' view, the trait must be an *engineering* adaptation that evolved by natural selection. Williams argued that group benefits do not, in general, exist *because* they benefit the group; that is, they do not have the appropriate causal history (see Brandon 1981, 1985, p. 81; Sober 1984, p. 262 ff.).

Implicit in Williams' discussion is the assumption that being a unit of selection at the group level requires two things: (1) having the group as an interactor, and (2) having a group-level engineering-type adaptation. That is, Williams combines two different questions, the interactor question and the manifestor-of-adaptation question, and calls this combined set *the* unit of selection question. These requirements for "group selection" make perfect sense given that Williams' prime target was Wynne-Edwards, who promoted a view of group selection that incorporated this same two-pronged definition of a unit of selection.

This combined requirement of "strong" (engineering) group-level adaptations in addition to the existence of an interactor at the group level is a very popular version of the necessary conditions for being a unit of selection within the group selection debates. David Hull claims that the group selection issue hinges on "whether entities more inclusive than organisms exhibit adaptations" (1980, p. 325). John Cassidy states that the unit of selection is determined by "Who or what is best understood as the possessor and beneficiary of the trait" (1978, p. 582). Similarly, Eldredge requires adaptations for an entity to count as a unit of selection, as does Vrba (Eldredge 1985, p. 108; Vrba 1983, 1984).

Maynard Smith (1976) also ties the engineering notion of adaptation into the version of the units of selection question he would like to consider. In an argument separating group and kin selection, Maynard Smith concludes that group selection is favored by small group size, low migration rates, and rapid extinction of groups infected with a selfish allele and that "the ultimate test of the group selection hypothesis will be whether populations having these characteristics tend to show 'self-sacrificing' or 'prudent' behavior more commonly than those which do not" (1976, p. 282). This means that the presence of group selection or the effectiveness of group selection is to be measured by the existence of nonadaptive behavior on the part of individual organisms along with the presence of a corresponding group-level adaptation. Therefore, Maynard Smith does require a group-level adaptation for groups to count as units of selection. As with Williams, it is significant that he assumes the *engineering* notion of adaptation rather than the weaker *selection-product* notion. As Maynard Smith puts it, "an explanation in terms of group advantage should always be explicit, and always calls for some justification in terms of the frequency of group extinction" (1976, p. 278; cf. Wade 1978; Wright 1980).

In contrast to the preceding authors, Sewall Wright separated the interactor and manifestor-of-adaptation questions in his group selection models (cf. Lewontin 1978; Gould and Lewontin 1979). Wright distinguishes between what he calls "intergroup selection," that is, interdemic selection in his shifting balance process, and "group selection for group advantage" (1980, p. 840; cf. Wright 1929, 1931).¹⁸ He cites Haldane (1932) as the originator of the term "altruist" to denote a phenotype "that contributes to group advantage at the expense of disadvantage to itself" (1980, p. 840). Wright connects this debate to Wynne-Edwards, whom he characterizes as asserting the evolutionary importance of "group selection for group advantage." He argues that Hamilton's kin selection model is "very different" from "group selection for the uniform advantage of a group" (1980, p. 841; see Arnold and Fristrup 1982; Damuth and Heisler 1987, 1988).

Wright takes Maynard Smith, Williams, and Dawkins to task for mistakenly thinking that because they have successfully criticized group selection for group advantage, they can conclude that "natural selection is practically wholly genic." Wright argues, "none of them discussed group selection for organismic advantage to individuals, the dynamic factor in the shifting balance process, although this process, based on irreversible local peak-shifts is not fragile at all, in contrast with the fairly obvious fragility of group selection for group advantage, which they considered worthy of extensive discussion before rejection" (1980, p. 841).

This is a fair criticism of Maynard Smith, Williams, and Dawkins. My diagnosis of this problem is that these authors failed to distinguish between two questions: the interactor question and the manifestor-of-adaptation question. Wright's interdemic group selection model involves groups only as interactors, not as manifestors of group-level adaptations. Further, he is interested only in the effect the groups have on organismic adaptedness and expected reproductive success. More recently, modelers following Sewall Wright's interest in structured populations have created a new set of genetical models that are also called "group selection" models and in which the questions of group adaptations and group benefit play little or no role.¹⁹

For a period spanning two decades, however, Maynard Smith, Williams, and Dawkins did not acknowledge that the position they attacked, namely, Wynne-Edwards', is significantly different from other available approaches to group selection, such as Wright's, Wade's, Wilson's, Uyenoyama's, or Lewontin's. Ultimately, however, both G. C. Williams and Maynard Smith recognized the significance of the distinction between the interactor question and the manifestor-of-adaptation question. In 1985 Williams wrote, "If some populations of a species are doing better than others at persistence and reproduction, and if such differences are caused in part by genetic differences, this selection at the population level must play a role in the evolution of a species," while concluding that group selection "is unimportant for the origin and maintenance of adaptation" (Williams 1985, pp. 7-8).

And in 1987, Maynard Smith made an extraordinary concession:

There has been some semantic confusion about the phrase "group selection," for which I may be partly responsible. For me, the debate about levels of selection was initiated by Wynne-Edwards' book. He argued that there are group-level adaptations . . . which inform individuals of the size of the population so that they can adjust their breeding for the good of the population. He saw clearly that such adaptations could evolve *only* if populations were units of evolution. . . . Perhaps unfortunately, he referred to the process as "group selection." As a consequence, for me and for many others who engaged in this debate, the phrase came to imply that groups were sufficiently isolated from one another reproductively to act as units of evolution, and not merely that selection acted on groups.

The importance of this debate lay in the fact that group-adaptationist thinking was at that time widespread among biologists. It was therefore important to establish that there is no reason to expect groups to evolve traits ensuring their own survival unless they are sufficiently isolated for like to beget like. . . . When Wilson (1975) introduced his trait-group model, I was for a long time bewildered by his wish to treat it as a case of group selection, and doubly so by the fact that his original model . . . had interesting results only when the members of the groups were genetically related, a process I had been calling kin selection for ten years. I think that these semantic difficulties are now largely over. (1987, p. 123)

Dawkins also seems to have rediscovered the evolutionary efficacy of higher-level selection processes in an article on artificial life. In this article, he is primarily concerned with modeling the course of selection processes, and he offers a species-level selection interpretation for an aggregate species-level trait (Dawkins 1989a). Still, he seems not to have recognized the connection between this evolutionary dynamic and the controversies surrounding group selection because in his second edition of *The Selfish Gene* (Dawkins 1989b) he had yet to accept the distinction made so clearly by Wright in 1980. This was in spite of the fact that, by 1987, the importance of distinguishing between evolution by selection processes and any strong adaptations produced by those processes had been acknowledged by the workers Dawkins claimed to be following most closely, Williams and Maynard Smith.

13.3.2 Genic Selection

One may understandably think that Dawkins is interested in the replicator question because he claims that the unit of selection ought to be the replicator. This would be a mistake. Dawkins is interested primarily in a specific ontological issue about benefit. He is asking a special version of the beneficiary question, and his answer to that question dictates his answers to the other three questions under consideration in this chapter.

Briefly, Dawkins argues that because replicators are the only entities that "survive" the evolutionary process, they must be the beneficiaries. What happens

in the process of evolution by natural selection happens *for their sake*, for their benefit. Hence, interactors interact for the replicators' benefit, and adaptations belong to the replicators. Replicators are the only entities with real agency as initiators of biochemical causal chains; hence, they accrue the credit and are the real units of selection.

Dawkins' version of the units of selection question amounts to a combination of the *beneficiary* question plus the *manifestor-of-adaptation* question. He does not somehow mistakenly think that he is answering the more predominant interactor question; rather, he argues that people who focus on interactors are laboring under a misunderstanding of evolutionary theory. One reason he thinks this, I submit, is that he takes as his opponents those who hold a combination of the interactor plus manifestor-of-adaptations definition of a unit of selection (e.g., Wynne-Edwards). Unfortunately, Dawkins thereby ignores those who are pursuing the interactor question alone; these researchers are not vulnerable to the criticisms he poses against the combined interactor-adaptation view.

I will discuss two aspects of Dawkins' own version of the units of selection issue. The first is his own preferred interpretation of the "real" units of selection problem. Here, I will attempt to clarify the key issues of interest to Dawkins and to relate these to the issues of interest to others. The second significant aspect of Dawkins' treatment of the units question is his characterization of the alternative views. The radical position Dawkins takes on units of selection makes more sense once his characterization of his opponents' questions becomes clear. In sum, he attributes to his opponents—sometimes incorrectly—a rich definition of a unit of selection involving not just the interactor question but also the beneficiary and manifestor-of-adaptation questions.

13.3.2.1 Dawkins' Preferred Question: Beneficiary

Dawkins believes that interactors, which he calls "vehicles," are not relevant to the units of selection problem. The *real* unit of selection, he argues, should be replicators, "the units that actually survive or fail to survive" (1982b, pp. 113–16). Organisms or groups as "vehicles" may be seen as the unit of *function* in the selection process, but they should not, he argues, be seen as the units of *selection* because the characteristics they acquire are not passed on (1982b, p. 99). Here he is following Williams' line. Genotypes have limited lives and fail to reproduce themselves because they are destroyed in every generation by meiosis and recombination in sexually reproducing species; they are only temporary (Williams 1966, p. 109). Hence, genes are the only units that survive in the selection process. The gene (replicator) is the real unit because it is an "indivisible fragment," it is "potentially immortal" (Williams 1966, pp. 23–4; Dawkins 1982b, p. 97).

The issue, for Dawkins, is "Whether, when we talk about a unit of selection, we ought to mean a vehicle at all, or a replicator" (1982b, p. 82). He clearly distinguishes the dispute he would like to generate from the group-versus-organismic selection controversy, which he characterizes as a disagreement "about the rival

claims of two suggested kinds of vehicles" (1982b, p. 82). In his view, replicator selection should be seen as an alternative framework for both organismic and group selection models.

There are two mistakes that Dawkins is not making. First, he does not deny that interactors are involved in the evolutionary process. He emphasizes that it is not necessary, under his view, to believe that replicators are directly "visible" to selection forces (1982b, p. 176). Once again, his "vehicles" are conceived as the units of function in the selection process (like interactors) but not as the units of selection.²⁰ Dawkins has recognized from the beginning that *his* question is completely distinct from the interactor question. He remarks, in fact, that the debate about group versus individual selection is "a factual dispute about the level at which selection is most effective in nature," whereas his own point is "about what we ought to *mean* when we talk about a unit of selection" (1982a, p. 46). He also realizes that genes or other replicators do not "literally face the cutting edge of natural selection. It is their phenotypic effects that are the proximal subjects of selection" (1982a, p. 47). He suggests changing his own terminology to "replicator survival" to avoid this confusion but does not seem to have followed up.

Second, Dawkins does not specify how large a chunk of the genome he will allow as a replicator; there is no commitment to the notion that single genes are the only possible replicators. He argues that if Lewontin, Franklin, Slatkin, and others are right, his view will not be affected (see Section 13.2.2). If linkage disequilibrium is very strong, then the "effective replicator will be a very large chunk of DNA" (Dawkins 1982b, p. 89). We can conclude from this that Dawkins is not interested in the replicator question at all; his claim here is that his framework can accommodate any of its possible answers.

On what basis, then, does Dawkins reject the questions about interactors? I think the answer lies in the particular question in which he is interested, namely, What is "the nature of the entity *for whose benefit* adaptations may be said to exist"?²¹

On the face of it, it is certainly conceivable that one might identify the beneficiary of the adaptations as—in some cases, anyway—the individual organism or group that exhibits the phenotypic trait taken to be the adaptation. In fact, Williams seems to have done just that in his discussion of group selection.²² But Dawkins rejects this move, introducing an *additional* qualification to be fulfilled by a unit of selection; it must be "the unit that actually survives or fails to survive" (1982a, p. 60). Because organisms, groups, and even genomes are destroyed during selection and reproduction, the answer to the survival question must be the replicator. (Strictly speaking, this is false; it is *copies* of the replicators that survive. He therefore must mean replicators in some sense of information and not as biological entities [see Hampe and Morgan 1988; cf. Griesemer in press]).

But there is still a problem. Although Dawkins concludes, "there should be no controversy over replicators versus vehicles. Replicator survival and vehicle selection are two aspects of the same process" (1982a, p. 60), he does not just leave the vehicle selection debate alone. Instead, he argues that we do not need the concept of discrete vehicles at all. I have shown elsewhere that if vehicles

are understood strictly as interactors, Dawkins (and everyone else) *cannot* do without them (Lloyd 1988, Ch. 7).

In Dawkins' analysis, the fact that replicators are the only "survivors" of the evolution-by-selection process automatically answers the question of who owns the adaptations. He claims that adaptations *must* be seen as being designed for the good of the active germ-line replicator for the simple reason that replicators are the only entities around long enough to enjoy them over the course of natural selection. He acknowledges that the phenotype is "the all important instrument of replicator preservation," and that genes' phenotypic effects are organized into organisms (that thereby may benefit from them during their own lifetimes) (1982b, p. 114). But because only the active germ-line replicators survive, they are the true *locus of adaptations* (1982b, p. 113). The other things that *benefit* over the short term (e.g., organisms with adaptive traits) are merely the tools of the real survivors, the real owners. Hence, Dawkins rejects the vehicle approach partly because he identifies it with the manifestor-of-adaptation question, which he has answered by definition, in terms of long-term beneficiary.²³

13.3.2.2 Dawkins' Characterization of Other Approaches

As discussed earlier, Dawkins is aware that the vehicle concept is "fundamental to the predominant orthodox approach to natural selection" (1982b, p. 116). He rejects this approach in *The Extended Phenotype*, claiming, "the main purpose of this book is to draw attention to the weaknesses of the whole vehicle concept" (1982b, p. 115). I will argue in the following paragraphs that his "vehicle approach" is *not* equivalent to what I have called the "interactor question" but encompasses a much more restricted approach.

In particular, when Dawkins argues against "the vehicle concept," he is arguing against the desirability of seeing the individual organism as the one and only possible vehicle. His target is explicitly those who hold what he calls the "Central Theorem," which says that *individual organisms should be seen as maximizing their own inclusive fitness* (1982b, pp. 5, 55). Dawkins' arguments are indeed damaging to the Central Theorem, but they are ineffective against other approaches that define units of selection more generally, that is, as interactors.

One way to interpret the Central Theorem is that it implies that the individual organism is always the beneficiary of any selection process; Dawkins seems to mean by "beneficiary" *both* the manifestor of an adaptation and that which survives to reap the rewards of the evolutionary process. He argues, rightly and persuasively, I think, that it does not make sense *always* to consider the individual organism to be the beneficiary of a selection process.

Note, however, that Dawkins is not arguing against the importance of the interactor question in general but rather against a particular definition of a unit of selection. The view he is criticizing assumes that the individual organism is the interactor, *and* the beneficiary, *and* the manifestor-of-adaptations. Consider his main argument against the utility of considering vehicles; the primary reason

to abandon thinking about vehicle selection is that it confuses people (1982b, p. 189). But look at his examples; their point is that it is inappropriate always to ask how an organism's behavior benefits that organism's inclusive fitness. We should instead ask, says Dawkins, "whose inclusive fitness the behavior is benefiting" (1982b, p. 80). He states that his purpose in the book is to show that "theoretical dangers attend the assumption that adaptations are for the good of . . . the individual organism" (1982b, p. 91).

So, Dawkins is quite clear about what he means by the "vehicle selection approach"; he advances powerful arguments against the assumption that the individual is always the interactor cum beneficiary cum manifestor-of-adaptations. This approach is clearly *not* equivalent to the approach to units of selection I have characterized as the interactor question. Unfortunately, Dawkins extends his conclusions to these other approaches, which he has, in fact, not addressed. Dawkins' lack of consideration of the interactor definition of a unit of selection leads to two grave problems with his views.

One problem is that he has a tendency to interpret all group selectionist claims as being about beneficiaries and manifestors-of-adaptations as well as interactors; this is a serious misreading of authors who are pursuing the interactor question alone. Consider, for example, Dawkins' argument that groups should not be considered units of selection:

To the extent that active germ-line replicators benefit from the survival of the group of individuals in which they sit, over and above the [effects of individual traits and altruism], we may expect to see adaptations for the preservation of the group. But all these adaptations will exist, fundamentally, through differential replicator survival. The basic beneficiary of any adaptation is the active germ-line replicator (1982b, p. 85).

Notice that Dawkins begins by admitting that groups can function as interactors and even that group selection may effectively produce group-level adaptations. The argument that groups should not be considered real units of selection *amounts to the claim* that the groups are not the ultimate beneficiaries. To counteract the intuition that the groups do, of course, benefit, in some sense, from the adaptations, Dawkins uses the terms "fundamentally" and "basic," thus signifying what he considers the most important level. Even if a group-level trait is affecting a change in gene frequencies, "it is still genes that are regarded as the replicators which actually survive (or fail to survive) as a consequence of the (vehicle) selection process" (1982b, p. 115). Dawkins argues, "a population . . . is not stable and unitary enough to be 'selected' in preference to another population" (1982b, p. 100).

Saying all this does not, however, address the fact that other researchers investigating group selection are asking the interactor question and sometimes also the manifestors-of-adaptations question rather than Dawkins' special version of the (ultimate) beneficiary question. Dawkins gives no additional reason to reject these other questions as legitimate; he simply reasserts the superiority of his own preferred units-of-selection question.

This is fair enough, provided that Dawkins keeps the different questions clear. But he seems instead to misinterpret the claims of group selectionists. For instance, Dawkins believes that group selectionists hold an expanded version of the Central Theorem, that is, that group-inclusive fitness is "that property of a group which will appear to be maximized when what is really being maximized is gene survival" (1982b, p. 187). Although Wynne-Edwards might be characterized as holding this view, Wade and Wilson certainly cannot. I think that Dawkins rejects their projects because he does not distinguish them from Wynne-Edwards's program (1978, pp. 73–4; 1982b, p. 115).

The other, more serious problem is that Dawkins fails to address, in his own theory, the interactor question itself: Which entities can and should be delineated as having traits or properties by means of which they interact with the environment in ways that affect the process of evolution by natural selection? In his desire to eliminate empirically and theoretically unjustified claims about beneficiaries of the selection process, Dawkins omits consideration of relevant questions about phenotypes that are addressed by other theoreticians. His attempt to circumvent the problems of a very restricted approach to selection that focuses on the organismic phenotype leads him, unfortunately, to gloss over a gap in his own view – specifically, how to delineate the "extended phenotype."

In discussing the extended phenotype, Dawkins is interested exclusively in traits that "might conceivably influence, positively or negatively, the replication success of the gene or genes concerned" (1982b, p. 234). Other incidental traits are "of no interest to the student of natural selection"; therefore, they are not included in the extended phenotype (1982b, p. 207). This makes perfect sense; he focuses on traits on which selection operates. But does he offer a principle for identifying these traits? Sterelny and Kitcher (1988) managed to distill a method of determining significant phenotype out of Dawkins. It turns out, not surprisingly, that this method is a simple version of the same principle widely used to delineate *interactors* by those theorists working on the (pure) interactor question (Lloyd 1988, Chapter 7). Hence, Dawkins can accommodate a viable method for delineating the extended phenotype but only through landing himself squarely in the middle of the interactor debate.

In conclusion, Dawkins' objections are effective against a particular view of the units of selection in which the unit is an interactor plus the beneficiary plus the manifestor of an adaptation. These objections are ineffective, however, against the more sophisticated views about units of selection widely held among the geneticists developing hierarchical selection models based on the interactor question.

The tension between Dawkins' picture of his opponents and the actual range of views they hold has led to an unfortunate and severe case of arguing at cross-purposes. The genic selectionists never actually make contact with some of their supposed opponents, and the hierarchical modelers similarly fail to realize that the appropriately limited version of the genic selectionist claims is no threat to them. Dawkins' concern to establish the ontological priority of genes over

the perceived theoretical hegemony of individual organisms falls on deaf ears among the geneticists, who do, after all, provide the inspiration for Dawkins' view in the first place.

13.3.3 Species Selection

Ambiguities about the definition of a unit of selection have also snarled the debate about selection processes at the species level. I argue in this section that a combination of the interactor question and the manifestor-of-adaptation question (in the engineering sense) led to the rejection of research aimed at considering the role of species as interactors, *simpliciter*, in evolution. Once it is understood that species-level interactors may or may not possess design-type adaptations, it becomes possible to distinguish two research questions: Do species function as interactors, playing an active and significant role in evolution by selection? and Does the evolution of species-level interactors produce species-level engineering adaptations and, if so, how often?

For most of the history of the species selection debate, these questions have been lumped together; asking whether species could be units of selection meant asking whether they fulfilled *both* the interactor and manifestor-of-adaptation roles. For example, Vrba used Maynard Smith's treatment of the evolution of altruism as a touchstone in her definition of species selection (1984). Maynard Smith argued that kin selection can cause the spread of altruistic genes but that it should not be called group selection (1976).²⁴ Vrba agreed that the spread of altruism should not be considered a case of group selection because "there is no group aptation involved; altruism is not emergent at the group level" (1984, p. 319; Maynard Smith gives different reasons for his rejection). This amounts to assuming that there must be group benefit in the sense of a design-type group-level adaptation. Vrba's view was that evolution by selection is not happening at a given level unless there is a benefit or adaptation at that level. That is, her definition of a unit of selection is a combination of an interactor and a manifestor-of-adaptations. She explicitly equates units of selection with the existence of an adaptation at that level (1983, p. 388); furthermore, it seems that she has adopted the stronger *engineering* definition of adaptation.

Eldredge also argues that species selection does not happen unless there are species-level adaptations (1985, pp. 196, 134). Eldredge rejects certain cases as higher-level *selection processes* because "frequencies of the properties of lower-level individuals which are part of a higher-level individual simply do not make convincing higher-level adaptations" (1985, p. 133).

Vrba, Eldredge, and Gould all defined a unit of selection as requiring an emergent, adaptive property (Vrba 1983, 1984; Vrba and Eldredge 1984; Vrba and Gould 1986). In my analysis, this amounts to asking a combination of the interactor and manifestor-of-adaptations question.

But consider the lineage or species-wide trait of variability. Although this may come as a surprise to some, treating species as interactors has a long tradition (Dobzhansky 1956, Thoday 1953, Lewontin 1958). If species are conceived

as interactors (and not necessarily manifestors-of-adaptations), then the notion of species selection is not vulnerable to Williams's original antigroup-selection objections.²⁵ The old idea was that lineages with certain properties of being able to respond to environmental stresses would be selected for, that the trait of variability itself would be selected for, and that it would spread in the population of populations. In other words, lineages were treated as interactors. The earlier researchers spoke loosely of adaptations, where adaptations were defined in the weak sense as equivalent simply to the outcome of selection processes (at any level). They were explicitly *not* concerned with the effect of species selection on organismic level traits but with the effect on species-level characters such as speciation rates, lineage-level survival, and extinction rates of species. I have argued, with Gould, that this sort of case represents a perfectly good form of species selection even though some balk at the thought that variability would then be considered, under a weak definition, a species-level adaptation (Lloyd and Gould 1993, Lloyd 1988).

Vrba has also recognized the advantages of keeping the interactor question separate from a requirement for an engineering-type adaptation. In her more recent review article, she has dropped her former requirement that, in order for species to be units of selection, they must possess species-level adaptations (1989). Ultimately, her current definition of species selection is in conformity with a simple interactor interpretation of a unit of selection (cf. Damuth and Heisler 1988, Lloyd 1988).

It is easy to understand how the two-pronged definition of a unit of selection – as interactor and manifestor-of-adaptation – held sway for so long in the species selection debates. After all, it dominated much of group selection debates until just recently. And I have argued that some of the confusion and conflict over higher-level units of selection arose because of an historical contingency – Wynne-Edwards implicit definition of a unit of selection and the responses it provoked.

13.4 Conclusion

It makes no sense to treat different answers as competitors if they are answering distinct questions. I have offered a framework of four questions with which the debates appearing under the rubric of “units of selection” can be classified and clarified. I follow Dawkins, Hull, and Brandon in separating the classic question about the level of selection or interaction (*the interactor question*) from the issue of how large a chunk of the genome functions as a replicating unit (*the replicator question*). I also separate the interactor question from the question of which entity should be seen as acquiring adaptations as a result of the selection process (*the manifestor-of-adaptations question*). In addition, I insist that there is a crucial ambiguity in the meaning of *adaptation* that is routinely ignored in these debates: adaptation as a selection product and adaptation as an engineering design. Finally, I suggest distinguishing the issue of the entity that ultimately benefits from the selection process (*the beneficiary question*) from the other three questions.

I have used this set of distinctions to analyze leading points of view about the units of selection and to clarify precisely the question or combination of questions with which each of the protagonists is concerned. I conclude that there are many points in the debates in which misunderstandings may be avoided by a precise characterization of *which of the* units of selection questions is being addressed.

13.5 Acknowledgments

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Notes

1. Mitchell also argues for the importance of keeping the interactor issue separate from issues involving replicators (1987).
2. For some of the pivotal arguments in the debates, see Brandon 1982, 1985, 1990; Dawkins 1978, 1982a,b, 1986; Hull 1980; Lewontin 1970; Maynard Smith 1964, 1976; Sober 1984; Sober and Lewontin 1982; Wade 1978, 1985; Wilson 1975, 1980; Wright 1980.
3. I have found nearly two hundred references to papers and books by biologists and philosophers that treat what is called here “the interactor question” (Lloyd 1988/1994); this represents just a fraction of the literature on the topic. The second most prominent interpretation of “the units of selection” question is “the replicator question” discussed in Section 2.2.
4. For example, Arnold and Frisrup 1982; Colwell 1981; Craig 1982; Crow and Aoki 1982; Crow and Kimura 1970; Damuth and Heisler 1988; Hamilton 1975; Heisler and Damuth 1987; Lande and Arnold 1983; Li 1967; Ohta 1983; Price 1972; Uyenoyama 1979; Uyenoyama and Feldman 1980; Wade 1978, 1980, 1985; Wade and Breden 1981; Wade and McCauley 1980; Wilson 1983; Wilson and Colwell 1981; Wimsatt 1980, 1981. See discussion in Lloyd 1988.
5. See Aoki 1982; Boorman and Levitt 1973; Fisher 1930; Ghiselin 1974; Leigh 1977; Levin and Kilmer 1974; Maynard Smith 1964, 1976; Uyenoyama 1979; Williams 1966.
6. See Lloyd 1988, Chapter 4.
7. For example, Arnold and Frisrup 1982; Brandon 1982; Colwell 1981; Damuth and Heisler 1988; Eldredge 1985; Griesemer and Wade 1988; Heisler and

- Damuth 1987; Lewontin 1970; Lloyd 1986, 1988, 1989; Sober 1981, 1984; Sober and Lewontin 1982; Vrba and Gould 1986; Wade 1985; Wilson 1980; Wimsatt 1980, 1981.
8. See the models cited in n.5 above for various technical approaches to expressing this special relation between fitness and trait.
 9. Lewontin 1970, 1974; Franklin and Lewontin 1970; Slatkin 1972; see discussion in Wimsatt 1980; Brandon 1982.
 10. The sense of agency assumed by Dawkins is worth investigating in detail. I will not, however, address this issue directly here. See Griesemer and Wade 1988. Related issues are discussed in Section 3.2.
 11. Brandon (1985) argues that such a view, which separates the level of adaptation from that of beneficiary, cannot be explanatory. Although I sympathize with Brandon's conclusions, they follow only under his set of definitions, which Dawkins and other genic selectionists would certainly reject.
 12. For explicit assumptions that being a unit of selection involves having an adaptation at that level, see Brandon 1982, 1985; Burian 1983; Mitchell 1987; Maynard Smith 1976; Vrba 1984.
 13. Oddly, Williams writes, "natural selection would produce or maintain adaptation as a matter of definition" (1966, p. 25; cf. Mayr 1976). However, Williams is committed to an engineering definition of adaptation (personal communication 1989).
 14. For example, Williams 1966; Bock 1980; Dunbar 1982; Ghiselin 1974; Gould and Lewontin 1979; Hull 1980; Lewontin 1978; Mayr 1978.
 15. Note that Williams says that "natural selection would produce or maintain adaptation as a matter of definition" (1966, p. 25; cf. Mayr 1976). This comment conflicts with the conclusions Williams draws in this discussion of Waddington; however, Williams later retracts this bithorax analysis (1985).
 16. Similarly for Maynard Smith (1964).
 17. Hence, Williams is here using the term *benefit* to signify the manifestation of an adaptation at the group level.
 18. It is worth remembering at this point that under Wright's view, interdemic group selection provided the means for attaining greater organismic adaptation; groups that are favored are "those local populations that happen to have acquired superior coadaptive systems of genes" (1980, p. 841).
 19. For example, Damuth and Heisler 1987; Heisler and Damuth 1988; Slatkin and Wade 1978; Uyenoyama 1979; Uyenoyama and Feldman 1980; Wade 1978, 1985; Wilson 1983.
 20. Hull has also argued that his own "interactors" and Dawkins' "vehicles" are not the same things (1980).
 21. (1982b, p. 81, my emphasis; cf. pp. 4, 5, 52, 84, 91, 113, 114). Compare an alternative formulation of Dawkins' central question: "When we say that an adaptation is 'for the good of' something, what is that something? . . . I am suggesting that the appropriate 'something,' the 'unit of selection' in that sense, is the active germ-line replicator" (1982a, p. 47). This particular formulation, I think, asks two questions, one about who the beneficiary of the selection process is and one about who possesses adaptations. Griesemer and Wimsatt's studies (1989) on Weismannism are of great help here.
 22. Note that Williams, even though he "keeps his books" in terms of genes, argued against the notion that particular group traits were group adaptations *because* these group traits are not properly understood as *benefiting the group* in the proper historical selection scenario (Williams 1966).

23. Mitchell arrives at a similar conclusion through different arguments. She highlights the impact of the notion of adaptation that seems to depend on the roles that Dawkins assigns to replicators (1987, pp. 359–62).
24. Again, this was because the groups were not interpreted as possessing design-type adaptations *themselves*.
25. As Williams himself has acknowledged, in a discussion on species selection: "The answer to all these difficulties must be Lloyd's . . . idea that higher levels of selection depend, not on emergent characters, but on any and all emergent fitnesses" (1992, p. 27).

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