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EVOLUTION, PHENOTYPIC SELECTION, AND THE UNITS OF SELECTION*

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In recent years philosophers have attempted to clarify the units of selection controversy in evolutionary biology by offering conceptual analyses of the term 'unit of selection'. A common feature of many of these analyses is an emphasis on the claim that units of selection are entities exhibiting heritable variation in fitness. In this paper I argue that the demand that units of selection be characterized in terms of heritability is unnecessary, as well as undesirable, on historical, theoretical, and philosophical grounds. I propose a positive account of the proper referent of the term 'unit of selection', distinguishing between the processes of evolution and phenotypic selection. The main result of this analysis is greater clarity about the conceptual structure of evolutionary theory.

1. Introduction. That evolution can proceed in the absence of natural selection is now a commonplace. Evolution can result from such nonselective processes as drift, mutation, inbreeding, and so forth. That natural selection can proceed in the absence of evolution has more recently become widely appreciated. Stabilizing selection, for example, is a process in which deviants from an optimal value of a character are selected against, thus maintaining gene frequencies at equilibrium in a population. As John Endler puts it, "Natural selection is a process that results from biological differences among individuals, and which may give rise to cumulative genetic change or evolution, but does not guarantee it" (Endler 1986, p. 26). Evolution and natural selection are therefore understood to be *contingently* related processes. It is the conjunction of the two processes—evolution by natural selection—which is held to account for much of the diversity we encounter in the living world. Carefully distinguishing between the two closely related processes has contributed to improvements in the articulation of evolutionary theory, and consequently to a clearer understanding of the causes of biological phenomena.

The distinction between evolution and natural selection is an important one, but it does not go quite far enough. Natural selection itself is a complex process which can be resolved into its constituent subprocesses.

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Doing so is essential for the identification of units of selection. In this paper I argue that units of selection should be identified with those entities that causally contribute to the subprocess of *phenotypic selection,* regardless of whether such entities *also* causally contribute to the distinct processes of evolution and natural selection. A consequence of this view is that units of selection need not be characterized in terms of heritable variation in fitness. Adopting a distinction made recently by Maynard Smith, I distinguish between units of selection and units of evolution. I then show how this distinction throws light on historical, theoretical, and philosophical aspects of the units of selection controversy.

2. Heritability. For a set of biological entities to evolve by natural selection there must be biological *differences* among the entities that affect their ability to survive and/or reproduce. Variance in *fitness* is thus a necessary condition for evolution by natural selection. But it is not a sufficient condition. There must also be a correlation between the properties of parents and offspring, so that the results of selection in one generation are passed on to the next generation. There must be *heritability*. In terms of geneticist Richard Lewontin's influential analysis, "The generality of the principles of natural selection means that any entities in nature that have variation, reproduction, and heredity may evolve" (Lewontin 1970, p. 1).

Several authors (for example, Wimsatt 1980, 1981; Lloyd 1986) writing on the units of selection controversy have argued that Lewontin's criteria for entities in nature to *evolve* also isolate requirements for an entity to be a *unit of selection*. Thus Wimsatt: "These principles give necessary conditions for an entity to act as a unit of selection". He goes on to say, "The three conditions must all be met by the same entity, in a way that can be summarized by saying that entities of that kind must show *heritable variance in fitness*" (Wimsatt 1980; reprinted in Brandon and Burian 1984, p. 102). These conditions, however, fail to be *sufficient* for an entity to be a unit of selection. Any entity displaying heritable variance in fitness is either a unit of selection or is *composed out of* units of selection. In particular, Wimsatt argues, the entities which are to be identified as units of selection must exhibit heritable *context-independent* variance in fitness among entities at that level which does not appear as heritable context-independent variance in fitness at some lower level (Wimsatt 1981, p. 144).

Context-independence is important, we are told, because only the context-independent variance in fitness is *heritable*. Variance in fitness which is context-*dependent* is destroyed when the context changes, and thus cannot be passed on to offspring. For example, phenotypic variance in fitness which is due to environmental factors is not passed on to offspring, although such offspring may exhibit it if the environment is the same as that occupied by their parents (Falconer 1981). Likewise, phenotypic variance due to genotype-environment interaction, or due to epistatic interactions among genes, is not heritable in the strongest sense, because such variance exists in virtue of contextual factors which may well change from parents to offspring. 'Heritability', in the sense in which population biologists use the term, denotes the contribution that *additive genetic variance* contributes to the total phenotypic variance. Phenotypic variance in a particular trait is said to be additive when it is due simply to the summed effects of each of a number of individual alleles taken separately. Heritability, and hence additive genetic variance, are closely related to the rate of evolution. R. A. Fisher's Fundamental Theorem of Natural Selection states (roughly) that the rate of evolution is proportional to the additive genetic variance of the population (Fisher 1930). More precisely, the rate at which a trait is evolving in a population increases as the product of its heritability and the intensity of the selection forces. When a term representing heritability is combined with a term representing a selection coefficient, the resulting model determines the rate of evolution—a very interesting and important result, and one which provides the foundation for Wimsatt's account (Wimsatt 1981, p. 144).

I wish to claim that although heritability (in either the narrow population genetics sense or in some broader sense) is essential for evolution by natural selection, and, indeed, for natural selection without evolution, it is nonetheless *not* a requirement for identifying an entity as a unit of selection. To show this I will sketch an abstract hypothetical example in which selection occurs in virtue of nonheritable variation in fitness among organisms. This abstract example will be filled out with concrete biological detail in a later section. The example presented here is intended to fix ideas without immersing us in questions of empirical accuracy.

Suppose, for the sake of argument, that we have a population of organisms randomly distributed in a patchy environment, among which there is significant phenotypic variance in some component of fitness. In general, such phenotypic variance might be due to underlying genetic factors, due to environmental factors, or, most commonly, it would be a product of an interaction between genetic and environmental factors (Futuyma 1986, pp. 195–200). The phenotypic variance in the component of fitness in the present case is interesting because it is due *entirely* to the environment. That is, the genetic contribution to the variance in this component of fitness is 0.0, and the environmental contribution to the variance in this component of fitness is 1.0. The population of organisms is then subjected to a selection regime, with the result that a higher proportion of those organisms possessing the component of fitness in question survives than of those lacking it. These survivors then go on to mate and produce offspring.

In the case I've just described there would be phenotypic variation in fitness among the individuals in the population of organisms as well as a selective force acting on these organisms. As a consequence, there would be differential mortality among the organisms in virtue of biological properties they possess (or lack), and the frequency of traits in the population would change as a result. But, given the absence of a genetic basis for the variation in the biological property in question, there might well be no corresponding change in *gene frequencies* nor change in frequency of traits in the population from one generation to the *next*. There would be no *natural selection,* because there would be no invariable correlation between the traits that aided the survival of the parents and those that are represented in the offspring. On this scenario we have differential survival (and mortality) of organisms in virtue of the survival value of their biological properties, but, due to the absence of *heritability* for these properties, no natural selection. Still, I would claim that the entities involved in the process described above are *selected for* in virtue of biological properties they exhibit, and thus function as units of selection in that process. I conclude that heritability is *not* a necessary feature of a unit of selection.

It might be objected that the case I've described is an example of the operation of *chance* in biological phenomena, not a case of *selection* in any sense, the reason being precisely that there is no *invariable* correlation between traits that aided the survival of the parents and those represented in the offspring. This objection misses the point in at least two ways. First, the example does not stipulate that the cause of the differential mortality be some *unusual* event, such as a flood or an earthquake, which wipes out organisms regardless of their biological properties. The selecting agent can be as *frequent* as one likes, sifting the population many times each generation until either no organisms remain, or else until it ceases to be efficacious because the only organisms left are ones unaffected by this selective agent. Second, the very fact that differential mortality is a function of differential exemplification of a biological property precludes this from being an instance of chance. Chance (for example, random genetic drift) is a *nondiscriminating* sampling process, whereas selection is a preeminently *discriminating* sampling process (Beatty 1984; Shanahan 1989). It would be strange to call a process which systematically eliminates individuals not bearing a certain property, but spares those displaying it, a *chance* process. This is especially so when the two kinds of individuals are *randomly distributed,* as in the hypothetical population. I conclude that selection can operate on nonheritable properties of biological entities. Heritability and selection are distinct.

3. Phenotypic Selection. The biological motivation for making the distinction between heritability and selection comes from the need to separate distinct subprocesses constituting the two-step process of natural selection in order to determine what empirical role each subprocess plays, either individually or in conjunction with others, in producing biological phenomena. Endler (1986), following the practice of quantitative geneticists and animal breeders (Fisher 1930; Haldane 1954; Falconer 1981; Lande and Arnold 1983), divides the process of natural selection into the sequential subprocesses of "phenotypic selection" and "genetic response". "Phenotypic selection is the *within-generation* change in the trait distribution among cohorts . . . and is independent of any genetic system or genetic determination" (Endler 1986, pp. 12–13). The genetic response is the genetic change which results from phenotypic selection in combination with the genetic system. This latter subprocess involves the transmission of the results of phenotypic selection to the succeeding generation, and requires that such results be heritable. Both phenotypic selection and genetic response are necessary for natural selection; neither is sufficient by itself. "Phenotypic selection determines the distribution of traits during reproduction, but inheritance is required to transform the distribution into the next generation" (Endler 1986, p. 13).

Although *natural selection* requires both subprocesses, the actual *selection* involved takes place in the first subprocess—during phenotypic selection. For this reason natural selection is sometimes identified with phenotypic selection (for example, Lande and Arnold 1983). It is during this subprocess that entities interact with the environment and, in virtue of possessing certain biological properties, change the frequency of traits in the ensemble of entities. The genetic response subprocess, as described by Endler, is an essentially nonselective process which transmits the results of phenotypic selection to the next generation. Both processes are necessary for the evolution of adaptations, and thus entities which undergo the sequential subprocesses of phenotypic selection and genetic response are in a position to display adaptations. But entities which undergo phenotypic selection but do *not* have a corresponding genetic response, precisely in virtue of undergoing phenotypic selection, function as units of selection in an important biological sense.

4. Units of Selection and Units of Evolution. This claim, of course, rests on a novel definition of the term "unit of selection", one which, to the best of my knowledge, is first made explicit by John Maynard Smith (1987). He distinguishes between "units of selection" and "units of evolution". When we ask what are the biological entities that are selected for or against, we are asking about the units of selection. That is, units of selection are entities which, in virtue of biological properties they display, interact with the environment in a way that causes their survival and/or reproduction to be differential. The concept of a "unit of evolution" is more complex. "To qualify as a unit of evolution, it is not sufficient that an entity be selected for or against; it must have heredity" (Maynard Smith 1987, p. 121). More precisely, in order to be a unit of evolution, a biological entity must display the properties of multiplication, heredity, and variation. Such entities are important because, Maynard Smith argues, given these properties, they may evolve adaptations.

Maynard Smith's distinction between two kinds of units important in evolutionary theory is an extremely useful one. As he says, "[I]t is important to distinguish between the objects we can expect to evolve adaptations and those we cannot" (Maynard Smith 1987, p. 122). Because the primary motivation for distinguishing units of selection from units of evolution is that the latter are the entities that display *adaptations,* whereas the former do not necessarily do so, a more appropriate term might be "units of adaptation". However, because Maynard Smith has used the term "units of evolution" in print, and because it does capture an important concept, I will continue to use his term in this paper. Units of selection, then, are entities which, in virtue of biological properties they display, interact with the environment in a way that causes their survival and/or reproduction to be differential. Units of evolution are entities which, in virtue of displaying *heritable* variation in fitness, may evolve adaptations.

I am well aware that this distinction as I have described it still leaves unresolved the question of *which* biological entities are instances of each type of unit. Determining the correct answer to *this* question requires consideration of conceptual and empirical issues beyond the scope of this paper. My aim here is the more general one of delineating the *kinds* of entities that need to be distinguished before clarity can be achieved with respect to the identification of specific instances of units of selection (and evolution). With this aim in mind, I turn next to applications of this distinction.

5. Historical Applications. Adoption of the distinction between units of selection and units of evolution helps to clarify historical, theoretical, and philosophical aspects of the units of selection controversy. I discuss each of these aspects in turn, beginning with the historical.

Although disagreements about the units of selection can claim an ancestry going back to the corespondence between Charles Darwin and Alfred Russel Wallace (see Kottler 1985 for details), the units of selection *controversy* began in earnest in the mid-1960s with the publication of V. C.

Wynne-Edwards' *Animal Dispersion in Relation to Social Behaviour* (1962), and G.C. Williams' response in his *Adaptation and Natural Selection* (1966). As the title of Williams' book suggests, a focal point of the debate concerned adaptations, in particular the question of whether adaptations should be attributed to higher-level biological entities such as groups. Wynne-Edwards argued that in fact such adaptations are quite common in nature, for instance in the form of "epideictic displays" which serve to inform individuals of the census size of their population so that they can adjust their reproductive output accordingly, thus preventing the population from over-exploiting its resources and suffering a crash—and maybe extinction. Wynne-Edwards proposed "group selection" as the mechanism explaining the maintenance of such group adaptations. Groups in which individuals show reproductive restraint persist longer than, and may invade areas left vacant by, groups in which individuals do not exercise such restraint and as a consequence of resource depletion go extinct.

In an article published in *Nature* in 1963, Wynne-Edwards attempted to clarify some of the issues presented in his book of the preceding year. He emphasizes that group selection on his view accounts for group-level adaptations evolved for group (rather than for individual) benefit.

> The kinds of adaptations which make [overriding individual advantage] possible . . . belong to and characterize social groups as entities, rather than their members individually. This in turn seems to entail that natural selection has occurred between social groups as *evolutionary units* in their own right, favouring the more efficient variants among social systems wherever they have appeared, and *furthering their progressive development and adaptation*. (Wynne-Edwards 1963, p. 623; emphasis added)

He is quite clear that group-level fitness is not reducible to the summation of individual fitness values.

> Population fitness . . . depends on something over and above the heritable basis that determines the success as individuals of a continuing stream of independent members. It becomes particularly clear in relation to population homeostasis that social groups have highly important adaptive characteristics in their own right. (Wynne-Edwards 1963, p. 624)

The emphasis throughout is on group adaptations resulting from heritable differences between groups as social units.

Williams countered that most (or perhaps all) such supposed group adaptations could be explained in terms of individual organisms each behaving so as to maximize its own fitness. Fish do not swim in schools *because* doing so is good for the school, even though it might, as a matter of fact, be good for the school, but because each fish is doing what is good for *itself*. Schooling behavior is the product of individual adaptations. Thus there is no need to postulate group adaptations when the same facts can be explained more parsimoniously in terms of individual adaptations (Williams 1966, pp. 212–217). Because group selection was held to be the cause of group adaptations, Williams' arguments against the latter were held to count equally against the former. Largely as a result of his critique, group selection explanations fell into disrepute.

More recently, however, D. S. Wilson (1975, 1979, 1980, 1983) has done much to revive the group selection debate by defending his "structured deme" model of "intrademic group selection". The model concerns organisms whose interactions with each other during some part of their life history take place within small local populations. Wilson calls such local populations "trait-groups". Mosquito larvae occupying different pitcher plants, bark beetles inhabiting different trees, and young birds being raised in the same nest are examples he mentions (1980, p. 21). After a period of interaction, the trait-groups dissolve, the individuals in each dispersing into the global population to mate. Mating in the global population is essentially random with respect to previous trait-group membership (that is, panmixia obtains). The cycle can then begin again: the pitcher plant mosquito, for example, will lay its eggs in another pitcher plant, and a new local population of larvae will have been founded.

Wilson then asks us to consider how gene frequencies in the global population might be affected by this cycle of within-trait-group interaction and dispersal into the global population. Changes in gene frequencies within each trait-group are a product of individual selection operating within each trait-group. Changes in gene frequencies in the post-dispersal global population are a product of the relative contributions each trait-group makes to the global population when it dissolves as well as continuing individual selection. Trait-group contributions to the post-dispersal global population need not be equal.

> Consider a genotype whose activities increase the productivity of its local population without, however, changing the gene frequency within the population. Populations with a high frequency of this genotype will be more productive than those with a low frequency, and will differentially contribute to the pool of dispersers. The genetic compositions of the dispersers will be biased toward the genotype that increases the productivity of its group, and this bias is carried into all groups colonized by the dispersers. (Wilson 1980, p. 19)

In summary, by introducing the concept of structured demes (that is, a global random-mating population broken up into local groups of interacting individuals), Wilson argues that natural selection becomes sensitive, not only to the fitness of individuals relative to each other in their local populations, but also to the productivity of local populations relative to each other in the global population. "This latter component may be regarded as natural selection on the level of populations, or *group selection*" (Wilson 1980, pp. 19–20; emphasis in original).

Wilson's model describes a group process which is similar to the group process envisioned by Wynne-Edwards in an important respect. In both processes the subdivision of a global population into local groups contributes to the increased representation of certain alleles in the global population. In both processes groups interact with their environments (which may include other groups) in ways that cause their persistence and/or multiplication to be differential. *In both processes groups function as units of selection.* But the substantial *differences* between the two models of "group selection" are worth noting as well.

An obvious difference is that whereas the mechanism for Wynne-Edwards' model is differential group *extinction,* the mechanism for Wilson's model is differential trait-group *productivity*. Maynard Smith (1982, p. 30) suggests the terms "group-extinction selection" and "trait-group selection" to mark this distinction. A more important difference, however, is that whereas Wynne-Edwards' groups exhibit group *adaptations,* Wilson's trait-groups do not.

An adaptation is a property of a biological entity whose existence is explained by reference to the selective advantage the property conferred on the biological entity's ancestors. Adaptations are not just properties conducive to fitness. They are phenotypic traits that have evolved as a direct product of natural selection (Williams 1966; Lewontin 1978; Brandon 1981; Gould and Vrba 1982). In this sense, adaptations need not even benefit the biological entities presently displaying them, if the environment the entity finds itself in is different from that in which the property was selected for among its ancestors. For a biological entity to possess a property as an adaptation, it must have inherited it from its progenitors, but it need not increase the fitness of its present possessor.

Wynne-Edwards' groups display adaptations (for example, conservative resource utilization, reproductive restraint) in virtue of being the direct descendents of groups which benefitted from the possession of such properties. Groups displaying such adaptations give rise to subsequent groups displaying the same adaptations, while groups lacking such adaptations go extinct. Wynne-Edwards' groups display heritable variation in group fitness. In his own words, they are "evolutionary units", or what are here being called *units of evolution*.

Wilson's trait-groups, on the other hand, because they are assembled anew each generation from the global population, cannot be identified as the descendents of specific trait-groups in the previous generation. A given trait-group might be composed of individuals descended from many (or all) of the trait-groups in the previous generation. Trait-groups do not inherit their group beneficial characteristics directly from other trait-groups. They display characteristics affecting group productivity in virtue of properties that increased the fitness of the ancestors of their constituent *organisms* in previous generations. The adaptations associated with differential trait-group productivity, if there are such, are individual adaptations rather than group adaptations. A concise way of stating this is that Wilson's trait-groups do not display heritable variation in group fitness. Unlike Wynne-Edwards' groups, they are *not* units of evolution.

Although he acknowledges important differences between his model and Wynne-Edwards', Wilson says that, "it would be a pity to avoid calling it group selection simply because that term has been applied to a different conception of groups in the past" (Wilson 1979, p. 609). But it is precisely because there *are* important differences between the two conceptions of groups that it is crucial to distinguish between them. Present in Wynne-Edwards' envisioned process of group selection, but lacking in Wilson's model, are group adaptations. An important historical development has taken place in models of group selection. Distinguishing between groups as units of selection and groups as units of evolution helps to clarify the precise nature of this historically significant development.

6. Theoretical Applications. The distinction between units of selection and units of evolution is not just of historical interest. It has some interesting applications in contemporary biological theory as well. The abstract hypothetical example presented earlier (section 2) in which organisms are selected on the basis of environmentally caused variance in fitness is an example of phenotypic selection without a corresponding genetic response. Organisms would not be expected to evolve adaptations through such a process. They would be units of selection, but not units of evolution. Here I will add some concrete biological detail to the formal possibility sketched earlier.

Recall that Wynne-Edwards argued that groups which over-exploit their resources are at a greater risk of extinction due to population crash than are those groups which maintain census size somewhat below the carrying capacity of the environment. The *mechanism* for population control proposed by Wynne-Edwards was reproductive restraint on the part of some (or all) members of the group. Such restraint requires a strong degree of altruism, since individuals must sacrifice some of their reproductive potential for the good of the group. The problem with this theory, as Williams and others since have shown, is in explaining how such altruistic restraint is maintained against invasion of the group by "selfish" individuals who reproduce to capacity at the expense of their neighbors.

As Wilson (1980) points out, however, the mechanism for population regulation need not be *voluntary* restraint on the part of individual organisms. Population regulation can be achieved by some individuals *interfering* with the activities of their neighbors.

> Perhaps the most general pathway for decreasing the cost of population regulation is interference behavior. Whereas in exploitation, organisms deal exclusively with their resources, in interference they deal directly with competitors. (Wilson 1980, p. 64)

Interference behavior is characterized by two general features. First, "All forms of interference derive their individual advantage from differential *suppression* of resource utilization" (Wilson 1980, p. 64). That is, some individuals gain by excluding other individuals from partaking of the resources. Eating a competitor is often an energy efficient means of preventing that individual from utilizing scarce resources. Second, "Nonheritable differences between individuals feature prominently in nearly all types of interference" (Wilson 1980, p. 64). The small, the young, and the disabled of all genotypes, in particular, are more likely to be the victims of interference. Size, age, and state of health are all variables affecting *vulnerability* to being interfered with which are not necessarily correlated with genotypic differences among individuals. Wilson illustrates these two features of interference using examples involving chemical inhibition, cannibalism, dominance, and territoriality. Here I will only discuss dominance, indicating how the relevant features of this behavior apply also to other behaviors, especially to territoriality.

In any primate troop in which there are a surplus of males relative to females, females will be a limiting resource with respect to which males will compete for reproductive access. Observations confirm our expectations: not all males compete equally well. The concept of *dominance* is used in behavioral ecology to describe a relationship between animals in which one individual (the dominant one) is able to supplant another (the subordinate one) from valuable resources. In primate troops there is often one or more dominant males that effectively monopolizes females, preventing subordinate males from mating. Such behavior satisfies the first feature of interference identified by Wilson: individual advantage results from differential suppression of resource utilization.

It appears that such behavior may, in *some* cases at least (and this is all that is necessary for our purposes), satisfy the second feature of interference as well—nonheritable differences between individuals. Disruption of the dominance hierarchy in a troop of Hamadryas baboons (by removing dominant males and then reintroducing them later) sometimes leads to a re-ordering of individuals higher or lower on the hierarchy

(Kummer 1971; Bachmann and Kummer 1980). Were differences in position in the hierarchy before disruption due to genetic differences between the individuals, one would expect, given that disruption doesn't affect genetic makeup, that the individuals that were dominant before would also be dominant after the disruption. Instead, dominance appears, sometimes at least, to be a function of the *history* of the troop, taken broadly to include past "ownership" of resources. If dominance with respect to control of females is correlated with fitness via increased reproductive opportunities, then there can ensue selection for being dominant, even though dominance in such cases constitutes a nonheritable difference between individuals.

It is easy to see how much the same conclusions might follow from an examination of territoriality, defined broadly as any enforced spacing behavior. Those individuals possessing a territory enjoy a certain "resource holding power" which excludes others from partaking of those same resources (Maynard Smith and Price 1973; Maynard Smith 1974; Parker 1974; Maynard Smith and Parker 1976). Initial acquisition of a territory proceeds on a "first-come first-served" basis, perhaps in virtue of having inherited the territory from parents. Competitions for territories are usually resolved merely on the basis of ownership, rather than on the basis of other properties of the individuals (Davies 1978; Krebs and Davies 1981). Ownership may be heritable in one sense: individuals whose parents controlled a territory may be more likely to inherit a territory than individuals with vagrant parents. But there is no reason to suppose that there are relevant *genetic* differences between the winners and losers in such cases. Selection may proceed entirely on the basis of genetically nonheritable variation in fitness resulting from the differential utilization of resources associated with the holding of a territory.

Consideration of interference behaviors such as dominance and territoriality suggests that there is a class of selection processes in which (genetic) heritability is not essential. The organisms participating in selection processes associated with these behaviors interact with the environment and with each other in ways that cause their survival and/or reproduction to be differential. They function as units of selection. But because such organisms do not display heritable variation in fitness with respect to the characteristics in question, they do not evolve adaptations with respect to such phenotypic properties. They are not units of evolution. Here is a theoretical context in which the distinction between units of selection and units of evolution clarifies the way in which behavioral characteristics may have great selective significance even though they have no effect on gene frequencies.

But if behaviors of the kind described here do not have a direct impact on gene frequencies, why should they be regarded as significant? They seem to have no evolutionary consequences, to be evolutionary dead-ends. The problem with this objection is that it assumes that the only significant selection processes in nature are those that result in evolutionary change. There is a danger in identifying the *reality* of processes occurring in nature with our ability to *measure* such processes. Without a change in gene frequencies across generations, selection will be difficult to detect. The ideal case for identifying the presence of a selection process is when gene frequencies show a consistent trajectory for a substantial period of time. Ideal though such cases may be, nature is not obliged to make things convenient for investigators.The fact that phenotypic selection is much harder to identify in the absence of "trail markers" like changes in gene frequencies or the evolution of adaptations is a function of our perceptual acuity, not a fact about real processes occurring in nature.

Population geneticists may have little interest in phenotypic selection apart from its direct consequences for *evolution,* but this is a function of the current research agendas of (some) biologists, not an indication of the importance of phenotypic selection in the causal structure of nature. *Ecologically,* it seems of the first importance. Wilson summarizes his discussion by saying, "In short, we have an event of great ecological importance that is phenotypically highly selective between individuals, yet is neutral from the genetic standpoint" (Wilson 1980, p. 72). If interference behavior of the kind described by Wilson represents pervasive processes occurring in nature, then, from a theoretical standpoint, phenotypic selection must be regarded as an important biological process worth studying.

7. Philosophical Applications. A final (brief) application of the distinction between units of selection and units of evolution concerns the recent philosophical literature on the units of selection controversy. A number of philosophers have proposed conceptual analyses of the term "unit (or level) of selection". As we have seen, some, such as Wimsatt (1980, 1981) and Lloyd (1986), require that units of selection be characterized as entities displaying heritable variation in fitness. Others, such as Sober (1984) and Brandon (1982) do not require that units (or levels) of selection be characterized in terms of heritability. Mayo and Gilinsky (1987) are the most explicit writers on this latter view. "Heritability is not strictly necessary for selection. . . . For sustained evolutionary change via selection, however, heritability is required" (Mayo and Gilinsky 1987, p. 515). As my remarks throughout this paper make clear, I think that the latter analyses make better sense, both historically and theoretically, than the former.

A challenge to this view is found in remarks made by Griesemer and

Wade (1988). They distinguish between (1) the causal process of evolution by natural selection, (2) the causal process of selection, and (3) units of selection. They acknowledge that although heritability is *not* necessary for *selection,* it is necessary for there to be an *evolutionary response* to selection. The possibility of there being an evolutionary response to selection seems to be the decisive consideration for them in conceptualizing units of selection, for they go on to insist that a unit of selection is to be characterized in terms of "the capacity to respond evolutionarily to selection, even if it never in fact does so" (p. 92). Accordingly, they endorse a refined "HVF [heritable variation in fitness] criterion" due to Lloyd (1986) which they say gives necessary and sufficient conditions for an entity to be a unit of selection.

But if the causal processes of evolution by natural selection and selection are worth distinguishing, then surely the kinds of biological entities that are capable of participating in these two processes are worth distinguishing as well. By including heritability in the requirements for a unit of selection, one excludes from the start consideration of entities which participate in phenotypic selection, but do not issue in any discernable evolutionary response. Such entities and the processes they participate in may be rare in nature or they may be common, but a *conceptual analysis* should not prejudice the issue in such a way that certain empirical questions are precluded from being asked. By carefully distinguishing between processes that require heritability and those that do not, we are in a better position to isolate the necessary and sufficient conditions an entity must display in order to function in each of these processes, and thereby to determine the empirical importance of each in the causal structure of nature. The distinction between units of selection and units of evolution clarifies the question of which properties an entity must possess in order to participate in different biological processes, and thus facilitates the empirical investigation of biological phenomena.

8. Summary/Conclusion. Empirical identification of units of selection in evolutionary biology has suffered from confusion concerning the necessary properties of a unit of selection. Starting from a distinction made explicit by Maynard Smith, I have argued that in identifying *units of selection* we are concerned with entities which, in virtue of biological properties they display, interact with the environment in a way that causes their survival and/or reproduction to be differential. That is, we are concerned with the entities participating in the subprocess of *phenotypic selection*. For such a process, entities need not exhibit heritable variation in fitness. When we inquire about the entities which display adaptations, we are asking which biological entities exhibit the properties they do because their ancestors participated in selection processes favoring those properties. The acquisition of adaptations requires a genetic response on the part of the entities in question. Entities displaying heritable variation in fitness are *units of evolution*.

The distinction between units of selection and units of evolution clarifies historical, theoretical, and philosophical aspects of the units of selection controversy. Whereas Wynne-Edwards and Williams were concerned with biological entities that evolve adaptations, recent debates, such as that concerning Wilson's trait-group model, concern the entities that function in group-mediated selection processes not issuing in group adaptations. The thesis that there may be significant selection processes in nature which do not have an impact on gene frequencies finds support in the analysis of interference behavior. Finally, by distinguishing between the concepts of units of selection and units of evolution, the empirical investigation of evolutionarily neutral but ecologically significant processes is encouraged.

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