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Units of selection

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"Understanding what kind of variation is possible and at what level selection occurs over those variations is what has driven the conversation about evolutionary biology at least since Darwin."¹

1. INTRODUCTION

At first glance, Darwin's theory of evolution by natural selection is among the simplest scientific theories ever advanced. Living things vary among themselves. These variations arise randomly, without regard to whether a given variation would be beneficial or not. Those living things with advantageous variations tend to stick around a bit longer than others, and give rise to more like themselves. Hence their numbers increase. That's the essence of Darwin's theory. What could be simpler? As Darwin's close friend Thomas Henry Huxley (1825-1895) is reported to have exclaimed after first encountering the idea of natural selection, "How extremely stupid of me not to have thought of that!"

Alas, the apparent simplicity of Darwin's theory is deceptive. From the very beginning Darwin's great idea has been subject to differing interpretations, and even now professional opinion is sharply divided on a range of fundamental issues. These are not challenges to Darwinism from without (like "Scientific Creationism") that question the entire project of giving naturalistic explanations of living things, but rather debates *within* Darwinism about the most basic causes, processes, and expected outcomes of natural selection. Central among these are debates about the nature and operation of natural selection.

Natural selection is the central explanatory principle of Darwinism. Selection explains why living things display complex adaptations, giving them the appearance of having been

intelligently designed. But life exists on many "levels," with biological systems organized hierarchically from genes and cells up through species and ecosystems. Selection is usually thought of as acting upon organisms. But does selection act at other levels as well? Does selection operate at levels "above" individual organisms? What has led biologists to argue about the correct "unit of selection," and how are such disputes best resolved?

Given the centrality of natural selection in Darwin's theory, it is of fundamental importance to understand how selection operates. This turns out to be considerably more difficult than it first seems. In a seminal article, Richard Lewontin noted that, "The generality of the principles of natural selection means that any entities in nature that have variation, reproduction, and heritability may evolve."² That seems clear enough. However, this seemingly straightforward observation, as Lewontin was well aware, harbors difficult problems. Consideration of these problems has led to one of the most vigorous controversies in contemporary evolutionary biology: the "units of selection" debate.³ Whereas some biologists have asserted that selection operates exclusively on individual organisms, others have advocated models according to which selection operates on other biological entities as well. A brief examination of "the group selection controversy" will help to bring some of the important issues into focus.

2. THE GROUP SELECTION CONTROVERSY

In order to explain certain puzzling biological phenomena that seemed to make little sense on the assumption that natural selection operates exclusively at the level of individual organisms, for example, the neuter castes of some eusocial insects, Darwin toyed with the idea of selection operating at the level of entire communities. The implications of this idea were profound. If selection operated at this more inclusive level, then the "beings for whose good natural selection works" might include groups as well as individual organisms. Selection operating at the group level could forge adaptations that benefit the group rather than each organism considered separately. Consequently, not every property of an individual organism need benefit that organism. Indeed, some organismic properties might even be detrimental to their immediate possessors, so long as they were sufficiently advantageous at the group level. Thanks to Darwin's invocation of group-level selection, for any biological phenomenon or

characteristic requiring an evolutionary explanation, one could ask whether it was selected and had thereafter evolved for individual or for group benefit.

Some later biologists welcomed Darwin's pluralistic conception of evolutionary theory with open arms, and made group selectionist explanations the cornerstone of their theorizing. A particularly influential example was Vero Copner Wynne-Edwards (1906-1997), who in 1962 published *Animal Dispersion in Relation to Social Behaviour*.⁴ In over six-hundred pages, he amassed evidence from a broad survey of the animal kingdom to show that animals actively regulate their population densities. Why such population regulation is necessary is explained early on: "[I]t must be highly advantageous to survival, and thus strongly favored by selection, for animal species (1) to control their own population-densities, and (2) to keep them as near as possible to the optimum level for each habitat they occupy."⁵

He realized that natural selection operating at the level of individual organisms could not bring about the kinds of social adaptations central to his theory, adaptations which benefit the group and entail subordination of the interests of individuals to those of the community. Selection operating on individuals would favor organisms that seek to maximize reproduction without regard for group welfare, inevitably leading to overexploitation of the habitat and population crash. Because such occurrences are rare, Wynne-Edwards concluded that some other evolutionary force must be operative. The mechanism for promoting the evolution of population regulation is identified as *group selection*. Groups that actively regulate their own numbers will tend to persist longer than groups that do not, and may spread to occupy areas left vacant by the latter. Wynne-Edwards thought this to be a widespread phenomenon in nature.

Animal Dispersion stimulated controversy from the moment of its appearance. As the history of this controversy has become canonized in recent years, G. C. Williams' book *Adaptation and Natural Selection* (1966) has often been seen as delivering the fatal *coup de grace* to Wynne-Edwards' theory. Williams was concerned with the relationship between selection and adaptation, in particular the question of whether adaptations should be attributed to higher-level biological entities, such as groups. Whereas Wynne-Edwards and other ecologists were often willing to invoke group-level adaptations at the drop of a hat, Williams insisted that "Adaptation is a special and onerous concept that should be used only where it is really necessary. When it must be recognized, it should be attributed to no higher a level of

organization than is demanded by the evidence."⁶ Williams argued that most (or perhaps all) supposed group adaptations could be explained in terms of the adaptations of individual organisms, each behaving so as to maximize its own fitness. Only if a population exhibits adaptations that promote group survival, which cannot plausibly be explained as an adaptation for individual reproductive success, can it be called an adapted population. If the group's continued survival is merely incidental to the operation of individual reproductive processes, however, then it is merely a population of adapted organisms.⁷

Although not the last critique of Wynne-Edwards' theory of group selection, for many biologists Williams' book marked the end of one era in evolutionary biology and the beginning of another. Together with other critical reviews, it convinced most biologists that group adaptations of the sort that Wynne-Edwards considered common were a chimera, and that group selection of the sort that he thought pervasive in nature was both unlikely and unnecessary.

Remarkably, in the 1970s group selectionist thinking "mysteriously rose from the dead."⁸ Why? First, it turned out that there were some cases that really did seem best explained as cases of group, rather than organism, selection (always a theoretical possibility that even Wynne-Edwards' staunchest critics conceded). Secondly, reaching back to models originally developed by Sewall Wright in the 1930s, biologists developed new models of group selection that were explicitly designed to avoid the sorts of problems that plagued earlier approaches. By the mid-1980s group selection had once again become mainstream.

David Sloan Wilson has done much to revive group selection by defending his "structured deme" model.⁹ Unlike Wynne-Edwards' model of group selection, Wilson's model does not require that individuals forego immediate gains in fitness for the sake of the long-term benefit of the group. In Wilson's model the benefits for other members of a group arising from an individual's actions are shared by the actor as well. He calls this "soft altruism." He considers the emphasis on strong altruism in the form of spectacular displays of self-sacrifice on the part of individuals, and the difficulty of explaining how this can evolve, to have been the chief impediments to taking group selection seriously. By focusing instead on behaviors which are individually as well as group advantageous, group selectionism can shake off an unnecessary restriction. Although models such as Wilson's are still controversial, most biologists are willing to admit that group selection of a sort can occur in nature under the right conditions.

3. GENIC AND KIN SELECTION

3.1 Kin selection

Group selection was one attempt to explain organismic behaviors that seemed to benefit others. But it was work on the social insects that led to a more encompassing explanation. The seeds of the solution can be found in the work of R. A. Fisher (1930)¹⁰ and J. B. S. Haldane (1932),¹¹ but it was W. D. Hamilton (1964) who offered the first compelling explanation for the sort of altruism found in the eusocial insects.¹² His idea was dubbed "kin selection." Hamilton's insight has generally been accepted as the correct explanation for a range of altruistic behaviors.

Kin selection is the idea that under certain conditions natural selection can favor a behavior that imposes a cost on the actor if it confers a benefit upon another organism that shares many of the same genes (e.g., a close relative). For example, if an organism possesses a gene that causes it to give aid to relatives who also possess a copy of that gene, then by giving such assistance the organism is assisting in the transmission of that gene (copies of which reside in another organism's body) into the next generation. In a sense, it doesn't matter whether the copies of one's genes are transmitted directly through producing offspring of one's own, or indirectly through the offspring of relatives. In either case, the genes in question are transmitted to the next generation. Kin selection thus provides a powerful explanation for how altruistic behaviors can be favored by natural selection. From the point of view of the behaving organism, such behavior is costly, but from the point of view of the gene, it is advantageous.

3.2 Gene selectionism

Adopting a gene-centered perspective helps to resolve some otherwise very thorny problems. The idea that at least *sometimes* natural selection operates directly at the level of individual genes is uncontroversial. But advocates of this view typically wish to claim much more than this. In addition to claiming that taking a gene-centered perspective solves a number of problems, they wish to assert that a gene-centered perspective is *always* the correct point of view to take. This latter view, that genes are the only true "units of selection," may be called "*gene selectionism*." Gene selectionism has come in for a good deal of criticism from biologists and philosophers, but there are several powerful arguments in its defense.

3.2.1 The a priori argument for gene selectionism

Gene selectionism has sometimes been defended using *a priori* arguments to the effect that genes, and only genes, have the requisite properties to function as units of selection, and thereby to be the ultimate beneficiaries of whatever adaptations exist. In his popular exposition of this approach, *The Selfish Gene* (1989), Richard Dawkins argues that genes can be thought of as repositories of information for constructing bodies (or "vehicles," in Dawkins' terminology).¹³ Differences in genes give rise to differences at the phenotypic level, resulting in the differential survival and/or reproduction of the genes responsible for those phenotypes. Genes are perpetuated to the extent that they produce phenotypic effects that give their possessors advantages over genes producing less advantageous phenotypic effects. Natural selection operates directly on phenotypes, but the indirect effects on genes leads to evolutionary change.

Dawkins argues that the unique properties of genes qualify them as the genuine "units of selection." Genes replicate themselves faithfully, exist in large numbers in virtue of the many copies of the same gene in a population, and persist for long periods of time. Genotypes (larger or smaller combinations of genes), organisms, and groups, on the other hand, are short-lived entities that quickly get broken down and reshuffled, exist in far fewer numbers, and "reproduce" themselves only in the most imperfect sense. Changes to an organism's body that are not encoded in the organism's genes exist only for the brief time that particular organisms exist. Genetic changes, on the other hand, can be passed on indefinitely. The point is that only genes get preserved from one generation to the next, and hence only genes have the properties necessary to be the units of selection and the "owners" of adaptations.

3.2.2 The explanatory scope argument for gene selectionism

A second kind of argument in support of gene selectionism points to its immense explanatory scope. Whereas some biological phenomena requiring a selectionist explanation can be explained either in terms of selection operating at the level of organisms or at the level of genes, *every* such phenomenon can be explained in terms of selection operating at the level of genes. Therefore, gene selectionism provides a much more general, and hence considerably more powerful, explanatory perspective in evolutionary biology.

3.3 Causality and representation

Gene selectionism has been a controversial thesis, and has thus met with its share of objections. In considering such objections, it is worth identifying two different versions of gene selectionism which in our discussion so far have not been distinguished. Each is associated with a particular thesis. According to *the causal thesis*, all selection is in fact selection at the level of individual genes. Expressed concisely, genes cause phenotypes, which then interact with the environment, resulting in the differential perpetuation of genes. Adaptations thus exist for the sake of genes. According to the *representation thesis*, on the other hand, regardless of the identity of the entities upon which selection actually operates, all selection can be *represented* in terms of selection at the level of genes. Even if selection acts directly on phenotypes, it is still true that only genes get passed on to subsequent generations, and in doing so serve as repositories of information. This is why all evolutionary change can be represented as changes in gene frequencies. Both versions of genic selectionism will be considered below as the two chief arguments in support of genic selectionism are critically evaluated.

3.3.1 The a priori argument undermined

Gene selectionists point out that organisms and groups are too ephemeral to be the beneficiaries of selection, because each is broken up and destroyed, if not in each generation, then after only a few generations. Only genes are passed on intact and hence persist from one generation to the next; therefore, only genes qualify as the beneficiaries of natural selection. This claim requires further scrutiny. If pressed, gene selectionists admit that it is not literally specific bits of genetic material that are passed on, but rather the *information* encoded in such bits of genetic material. But if so, then it can be claimed with equal justice that *phenotypic properties* persist and get passed on from one generation to the next. That is, an objection that could be leveled at gene selectionism is that certain *properties* of organisms have every bit as much right to be considered that which gets passed on to offspring as do their genes. In fact, they might have more right to be considered that which is preserved and passed on, because in many organisms (e.g., birds, primates, humans) there is intergenerational transmission of learned behaviors. Thinking of properties, rather than genes, as that which is passed on would include all those properties coded for by genes, and plus others. It would therefore be the foundation for a more

comprehensive account of evolutionary change. Quadrupeds pass along their quadrupedalism; animals with binocular vision pass on their binocularity; and so on. Darwin's theory is supposed to be a very general theory of evolution, applicable to life forms anywhere in the universe. Conceivably, there might be life forms elsewhere that do not use DNA or any genetic material, but instead pass along their characteristics via some other mechanism. Were we to encounter such creatures, we would recognize them as having evolved by a process of natural selection, despite the fact that they lack "genes" in the normal sense. All that is necessary for the transmission of information or properties from one generation to the next is suitable physical embodiment and a reliable copying mechanism. Genes represent one such possibility. There is no reason there could not be others. But if so, then the chief *a priori* argument in support of gene selectionism collapses.

3.3.2 Thrust and parry re the causal thesis

Whereas the representation thesis is often grudgingly conceded by critics of gene selectionism, the causal thesis has more frequently been vigorously challenged. They argue that although all evolutionary change can be *represented* in the currency of selection for or against individual genes, it is nonetheless false that all selection is causally *explainable* in terms of selection for or against individual genes. Gould puts the matter bluntly: "Selection simply cannot see genes and pick among them directly. It must use bodies as an intermediary. A gene is a bit of DNA hidden within a cell. Selection views bodies."¹⁴ According to this view, the whole organism, rather than the individual gene, is the unit of natural selection. Gene selectionism should therefore be thought of as merely a "bookkeeping" technique which fails to identify the *causes* of evolutionary phenomena.

Another common objection to the causal thesis of gene selectionism points out that the idea that there is a "gene for" some particular phenotypic characteristic relies on a misleading picture of biological causation. There is no "gene for blue eyes" because (i) blue eyes are the effect of a number of genes, and (ii) each gene can have multiple phenotypic effects. Between genes and phenotypes there are "one-many" (pleiotropic) and "many-one" (epistatic) effects. Consequently, selection cannot be discriminating amongst individual genes.

Gene selectionists respond that such objections miss the mark. What an expression like "gene for" means is that the presence or absence of a particular gene makes a difference at the phenotypic level. Dawkins develops this point by distinguishing between blueprints and recipes.¹⁵ The individual words in a cake recipe do not map onto particular bits of the finished cake, but replacing one word with another -- salt for sugar, for example -- will result in a very different final product. Any given gene may have multiple phenotypic effects. The selective advantage of having any particular gene is the net benefit conferred when all the effects of the gene are taken into account. Consequently, even if a simplistic understanding of the expression "gene for" is false, there is still an important sense in which all selection is selection for or against individual genes. Gene selectionism cannot be defeated so easily.

4. ASSIGNING FUNCTIONAL ROLES

At this point, the debate over gene selectionism seems to have reached a stalemate, with some biologists arguing that genes are the true "units of selection," whereas others deny this. Everyone agrees that genes are involved in natural selection in some way, and that genes are closely related to the organisms they "build." Part of the problem involves disentangling the respective causal roles of the various biological entities involved. This is complicated by the fact that often the fate of genes and that of organisms are closely linked, such that in many cases organism-centered and gene-centered approaches will coincide. In most instances, organism-centered and gene-centered approaches both predict that genes will cause phenotypic effects that are conducive to the survival and reproduction of the organisms that possess them. How can such ideas be used to resolve the controversy about the units of selection?

4.1 Replicators and interactors

According to David Hull, distinguishing between the entities that replicate their structures and produce bodies, on the one hand, and those that directly face selection, on the other, is essential for resolving the units of selection problem. That is, two kinds of entity are important for describing the operation of natural selection. First, for evolution by natural selection to take place, spatiotemporal sequences of replicates are necessary. In Hull's terminology, a *replicator* is defined as "an entity that passes on its structure largely intact in successive replications."¹⁶

Replication by itself, however, is insufficient. Some entities must interact causally with their environments in such a way as to bias their distribution in later generations. An *interactor* is defined as "an entity that interacts as a cohesive whole with its environment in such a way that this interaction *causes* replication to be differential."¹⁷ The relationship between an interactor and its environment is mediated by phenotypic properties that affect the interactor's biological success (as measured by survival and reproduction). "Selection" is then defined as "a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the relevant replicators."¹⁸

What are the advantages of drawing such distinctions? Hull holds that controversies have flourished because of ambiguity in the term "unit of selection." Sometimes this term is used to refer to the entities responsible for replication, at others to the entities responsible for interaction. When the distinction between replication and interaction is kept in mind, Hull believes, conceptual disagreements concerning *the* unit of selection are seen to be only apparent.

The replicator/interactor distinction is not intended to resolve all questions about the units of selection, however. Empirical questions will remain concerning which biological entities play each of these evolutionary roles. The distinction between replicators and interactors suggests that there are really two central empirical questions at issue in discussing the levels of selection: "[A]t what levels does replication occur, and at what levels does interaction occur?"¹⁹ There is widespread agreement that genes are paradigmatic replicators. Can other entities function as replicators? Hull notes that, "replication is concentrated at the lowest levels, primarily at the level of the genetic material," although perhaps also at the level of organisms and possibly colonies, but rarely higher.²⁰ Organisms and even single cells can sometimes function as replicators. On the other hand, one reason that organisms are not typically replicators is because in those organisms with sexual reproduction, in order for the structure of the organism to be copied, it must first pass through a gametic stage which is radically different from the adult organism. This is quite unlike the way in which genes replicate, according to which their structure is passed on directly in the form of exact copies.

Interactors, too, must meet certain ontological criteria. Foremost among these is that the entity must interact with its environment as a "cohesive whole." That is, interactors must be *individuals*, understood in a very specific sense. "By 'individual' I mean any spatiotemporally

localized entity that develops continuously through time, exhibits internal cohesiveness at any one time, and is reasonably discrete in both space and time."²¹ Organisms are paradigmatic individuals, but other biological entities displaying cohesiveness and internal organization, including populations and species, may qualify as well.

How does this analysis bear on the units of selection issue? In most selection processes, the replicators are genes. But if so, then selection processes must be distinguished on the basis of the interactors involved. In point of fact, this is the way that selection processes are usually distinguished. Organism selection is a process in which organisms interact with their environments (including each other), resulting in differential reproductive success among organisms. Group selection, at least as Wynne-Edwards conceived it, involves differential interaction between groups and their environmental resources. The question of "group selection" then becomes the question of whether groups have the requisite properties to function as interactors. This is an important start, but further questions must be addressed as well if we are to identify the beings "for whose good" natural selection works. Knowing that certain biological entities can function as interactors does not by itself tell us for whose good adaptations exist. In order to answer this fundamental question, further distinctions must be introduced.

4.2 Getting serious about functional roles

This is just what Elisabeth Lloyd sets out to do.²² Incorporating the Hull's distinctions, Lloyd (2000) distinguishes four different kinds of entities that play a role in the evolutionary process: interactors, replicators, beneficiaries, and manifestors of adaptations. "Interactors" are those individuals that respond directly to selection pressures via their phenotypic properties. "Replicators" are those entities that pass on their structures directly through replication. "Beneficiaries" are the entities that benefit in evolution; e.g., get more copies of themselves into the next generation; or those entities that benefit from adaptations. Finally, "manifestors of adaptations" are, as the name suggests, the entities that exhibit adaptations.

Lloyd argues that deploying these distinctions helps to further clarify questions about "the units of selection." For example, in the debates over group selection there are really at least two issues at stake: (i) Does selection ever operate on groups as cohesive wholes? (That is, do groups ever function as *interactors*?) (ii) Do groups ever manifest group-level adaptations that

are not better understood as simply a summation of the adaptations of lower-level entities, e.g., organisms? (That is, are groups ever *manifestors of adaptations*?) Whereas Wynne-Edwards proposed a model of group selection according to which groups function as both interactors and as manifestors of adaptations, Wilson's model of group selection suggests that groups can sometimes function as interactors (i.e., that group-level properties can be important in evolution), without also claiming that groups are either the beneficiaries of selection or the manifestors of adaptations. This much seems to be generally accepted. The contemporary units of selection debate tends to focus on the question of whether organisms or genes should be thought of as the beneficiaries of selection or the manifestor of adaptations. Lloyd's distinctions help to clarify these issues as well. In particular, her distinctions show that some gene selectionists conflate the various functional roles entities play in evolution. For example, Cronin (1991) tends to collapse the identity of interactors, replicators, manifestors of adaptations, and beneficiaries of adaptation, identifying genes as the all-purpose "units of selection" that serve all of these distinct functional roles.²³ Lloyd's analysis makes clear why this is problematic. Genes replicate, but then so do *some* organisms and *some* groups. Genes typically interact with the environment to influence their own survival only via adaptations associated with organismic phenotypes. It therefore makes at least as much sense to say that organisms are the manifestors of adaptations as it does to say that genes are. Finally, the question of the ultimate beneficiaries of adaptations remains open. The genes of a biologically successful organism benefit from that organism's success, but then so too does that organism. Identifying genes as "the units of selection" *simpliciter* provides a misleadingly simple account, and fails to acknowledge that there are alternative, equally plausible, ways of describing the dynamics of evolution.

As useful as Lloyd's distinctions are, they still leave open questions about *which* entities do, as a matter of fact, play each of the functional roles she identifies. As noted above, genes seem to be paradigmatic replicators. But organisms, and in some cases colonies seem to replicate after a fashion as well. Likewise, organisms and groups interact with their environments, but then so too do genes with their environments. Adaptations can be ascribed to organisms just as easily as they can be ascribed to genes. Finally, gene selectionists take genes to be the ultimate beneficiaries of natural selection, because they persist from one generation to the next, whereas phenotypes do not. But even if entire phenotypes, i.e., the total collection of properties

characterizing a given individual -- do not persist across the generations, particular phenotypic properties, especially those that are fitness-enhancing, do. For example, if a particular pattern of camouflage is fitness-enhancing, then this phenotypic pattern will get passed on and hence persist from one generation to the next. So one could as well focus on particular phenotypic properties as on individual genes.

Is there any way to transcend the approaches discussed thus far? There seem to be just two options: (1) adopt a "pluralistic" approach according to which selection can be modeled equally well as operating and forging adaptations at any of a number of distinct biological levels; or (2) abandon the idea that selection is properly conceived as acting on distinct levels, and embrace instead a "holistic" vision in which processes at various levels are integrated. Both approaches are worth examining.

5. PLURALISM AND HOLISM

Standard attempts to resolve the units of selection problem take for granted that the entities upon which selection operates can be identified with one or another of the entities constituting the biological hierarchy (e.g., genes, organisms, groups, etc.), and that a satisfactory analysis of a given selection process requires the identification of the unit(s) and level(s) of selection causally responsible for that process. Sterelny and Kitcher (1988) christen this view *Hierarchical Monism*. Hierarchical Monism embodies two distinct claims: (1) for any selection process there is just *one representation* that correctly captures the causal structure of that process, and (2) this representation depicts selection as operating on just *one level* of the biological hierarchy.

Sterelny and Kitcher reject this view. Not only is there no uniquely correct way of describing any selection process, but talk of "units of selection" is itself philosophically suspect. "Monists err," they write, "in claiming that selection processes must be described in a particular way, and their error involves them in positing entities, 'targets of selection', that do not exist."²⁴ Asking about the "real unit of selection" in a given case is based on a confusion, because selection events can be modeled in any of a number of different, equally correct ways (e.g., as acting on, or as benefiting, genes or organismic phenotypes, etc.). The way that one chooses simply depends upon one's methodological interests.

5.1 The pluralist option

In place of Hierarchical Monism, Sterelny and Kitcher propose a view they call *Pluralism*. Rather than assuming that for each process there is just *one* adequate representation, they maintain that for any process there are *many* adequate representations, but that processes are diverse in the kind of representations they demand. Whereas Hierarchical Monism recommends a "plurality of processes," each with its own model, Pluralism recommends "a plurality of models of the same process."²⁵ They conclude that, "We are left with the general thesis of pluralism: there are alternative, maximally adequate representations of the causal structure of the selection process."²⁶

Sterelny and Kitcher's Pluralism states an important fact: Many selection processes can be equally well represented by models depicting selection as operating on any of a number of distinct biological levels. It is a mistake to think that if a description of a selection process in terms of organismic properties is correct, then a description in terms of genic properties cannot be. As they note, for any given selection process, there might be any number of *equally good* descriptions. Nonetheless, Sterelny and Kitcher overstate their case when they claim that for any biological phenomenon in need of a selectionist explanation, there are *alternative, maximally adequate representations* of the causal structure of the selection process. To see this, consider a spider web. A well-constructed spider web benefits both the spider that made the web as well as the genes responsible for the relevant behaviors. On Sterelny and Kitcher's view, the evolution of spider webs could be represented with equal adequacy as a result of selection operating on spider-genes, *or* as selection operating on spiders. These are claimed to be alternative, maximally adequate representations of the causal structure of the selection process, each framed in terms of the entities on just one level of the biological hierarchy. But are they? Undoubtedly one can provide a partial account of the evolution of spider webs solely in terms of selection operating on the entities on just one level of the biological hierarchy, but a *maximally adequate representation* of the causal structure of this process would necessarily have to take into account the causal connections *between* entities on different levels of the biological hierarchy, without which the phenomenon under consideration could not have occurred at all. This is because *the causal connections between entities on different biological levels constitute part of the causal structure of the selection process*. Spider-genes partially cause spiders; spiders build webs; these webs

assist the spiders in passing along their genes to subsequent generations, and so on. Spider-genes, spiders, and webs exist in an interconnected causal nexus that taken as a whole results in the differential survival and/or reproduction that is natural selection. This suggests that for any selection event there is just one maximally adequate representation that correctly depicts the causal structure of each selection process, one which does so by taking into account the causal contributions of (and causal connections between) whatever entities are involved in the process. Once all such contributions are taken into account, then at most one such representation will be possible. But if so, then Pluralism of the sort defended by Sterelny and Kitcher is mistaken.

5.2 The holist option

Such considerations suggest a very different perspective on selection, adaptation, and the evolutionary process as a whole. These insights are developed most fully in the *developmental systems approach* to evolution.²⁷ The essential challenge to both gene selectionism *and* the attempt to distinguish distinct functional roles in evolution is straightforward: "Developmental systems theorists claim that there is no privileged class of replicators among the many material causes that contribute to the development of an organism -- that the entire replicator/interactor representation of evolution is refuted by the facts of developmental biology."²⁸ According to this alternative view, "Rather than replicators passing from one generation to the next and then building interactors, the entire developmental process reconstructs itself from one generation to the next via numerous interdependent causal pathways."²⁹ Genes are replicated, but the replication of genes is just one aspect of the replication of a life cycle. "Every element of the developmental matrix which is replicated in each generation and which plays a role in the production of the evolved life-cycle of the organism is inherited.... The process of evolution is the differential reproduction of variant life-cycles."³⁰ Entire developmental systems, rather than genes (for example), are thus the "units of natural selection".

Consider again the spider-web example. Spider genes may be thought of as embodying the "design instructions" for both spiders and webs. Webs are constructed by organisms executing these instructions. Web designs are in competition with one another for effectiveness in catching prey. Spider-genes are causally connected with spiders, web-building behavior, webs, and to the capture of prey, resulting in the differential propagation of genes, the spiders, and

webs. Selection in this case is operating on the entire gene-spider-web causal process. A maximally adequate representation of the causal structure of this selection process will include not only a description of how each of the entities involved in the process fares relative to other entities of the same kind (i.e., at the same level), but also how the entire causal chain contributes to the differential representation of genes, spiders, and webs in successive generations.

The basic arguments for this view are straightforward. Consider first an argument against gene selectionism. Genes can be the uniquely correct units of selection *only if* genes play some distinctive, privileged role in the development of the organism. But it is *false* that genes play such a role. First, organisms inherit more than genes from their parents. Besides the non-nuclear DNA that appears in mitochondria, some organisms inherit behaviors learned from parents or from other conspecifics. The distinctive song dialects of some birds, for example, are passed on from generation to generation, and are acquired only by juvenile birds being exposed to adult renditions of these dialects. Preferences for nest sites and nesting materials, as well, are acquired through early exposure as nestlings and juveniles. Such cases of "cultural transmission" are by no means restricted to vertebrates like birds. Genes obviously play a role in the development of adult song repertoire and nesting behavior, but not the only, or even necessarily the most important, role.

Secondly, the causal thesis associated with genic selectionism is simply false. Strictly speaking, genes, by themselves, produce nothing. Only genes working within a context of a complete developmental system can produce phenotypes. But if so, then genes, by themselves, ought not to be given privileged status as the units of selection.

Finally, the very idea of genes as the "replicators" in evolution breaks down when one considers that other biological entities (e.g., organisms) replicate in much the same way. In any case, it is entire developmental processes, not individuated biological entities, that replicate themselves. But if so, then the "replicator/interactor" distinction is also suspect.

In summary, in contrast to gene selectionists, developmental systems theorists see the entire "life cycle" as the fundamental unit of evolution. "A life cycle is a developmental process that is able to put together a whole range of resources in such a way that the cycle is reconstructed.... Organisms have life cycles, and so do groups like ant colonies. Variants on these life cycles compete with one another."³¹ This approach provides a very different perspective than

that insisted upon by gene selectionists. Genes are just one component of the complex developmental system. It can as well be said that genes exist in order to assist in the transmission of developmental systems (or of phenotypic properties) as it is to say that developmental systems exist for the sake of transmitting genes. All are bound together in integrated systems that fail to replicate should any essential component fail to function as designed by natural selection. Genes play an important, but not a privileged, role in this process.

5.3 Replicators strike back

Critics have generally applauded the insights of the Developmental Systems approach, while drawing attention to its weaknesses. Among the latter, the "boundary problem" has attracted special attention. Developmental Systems Theory emphasizes the "connectedness" of all parts of the developmental system. But what principled way is there to distinguish what is and is not relevant to a given developmental system? As some critics put it, "Everything causally connects with everything else.... So if developmental systems include everything causally relevant to development, they are too ill-defined to be a coherent active unit; they are too diffuse to be units of selection."³² Likewise, this approach requires the generation by generation reproduction of developmental systems, which presupposes that "generations" have distinct boundaries. But critics ask: "So when do generations begin and end: do we count from bird to bird, egg to egg, or nesting hole to nesting hole? Cycles of developmental resources are not necessarily in sync.... Is an ant-plant mutualism a single developmental system or several?"³³

Developmental Systems theorists are not without resources to respond at this point. In response to the boundary problems described above, they can choose to "bite the bullet" and take the holist perspective to its logical conclusion by agreeing that, in principle, anything might be relevant to a given developmental cycle. However, "interconnectedness of everything" no more counts against the Developmental Systems approach in biology than it does against the Newtonian research program in physics. One is always forced to be selective in deciding which factors to include in one's model. A similar response is available for deciding where one generation ends and another begins. Noting that there is no given line demarcating one generation from another simply reinforces the point that biological systems are integrated, continuously developing wholes. Finally, asking whether an ant-plant mutualism is a single

developmental system or several, rather than constituting a *reductio ad absurdum* of the Developmental Systems approach, actually highlights its potential for considering familiar biological phenomena in an entirely new light. For example, perhaps termite mounds with their elaborate air-conditioning system, their termite builders, and the cellulose-digesting protozoa that inhabit their guts should be viewed as components of the same developmental system that gets replicated generation after generation. Rather than asking which component of this system is the "real" unit of selection, the entire system can be fruitfully viewed as subject to selection.

6. CONCLUSIONS

Darwin maintained that "natural selection works solely by and for the good of each being."³⁴ But there are many "beings" involved in the evolutionary process. *By* whose and *for* whose "good" does natural selection work? As we have seen, the problem is much more difficult than it might at first appear. It has commonly been assumed that typically selection operates on individual organisms (and perhaps some groups), that adaptations "belong" to organisms (and perhaps some groups), and that genes (as measured by their representations in subsequent generations) are the ultimate beneficiaries of adaptations. As critics have pointed out, however, this perspective faces a number of serious difficulties, not the least of which is that upon closer analysis, genes do not seem to play quite the privileged role that is claimed for them. As Developmental Systems theorists point out, however, entire life cycles, not to mention specific phenotypic properties, are also "replicated," reappear generation after generation, and thus have equal right to be considered the beneficiaries of natural selection.

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