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Part I

Overview

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Evolution and Agency

A User's Guide

I OVERVIEW

Earlier work in philosophy of biology focused mostly on understanding the relationship between biology and the more basic sciences of physics and chemistry, and developing more subtle views on the major themes of philosophy of science – reduction, explanation and causation – based on a broader range of scientific practice. Those issues are still alive in the literature (see, for example, Dupre 1993; Rosenberg 1994), but in my view philosophy of biology acquired its contemporary character when the central debates shifted to issues internal to biology itself. The first such issue was the debate within evolutionary theory about the nature of selection. In his classic reconstruction of the Darwinian program, Mayr isolated five independent evolutionary theses: evolution has occurred; contemporary species have ultimately descended from at most a few earlier life forms; evolutionary change is typically gradual; species normally form when lineages split and the fragments diverge, and the mechanism of adaptive evolution is natural selection (Mayr 1991). Many of these ideas are no longer controversial. No-one within the community doubts the fact of evolution, nor that contemporary life is descendant from a single ancestor (or perhaps a few). Almost no-one doubts that natural selection has played some significant role in this process. But there continues to be much debate on the nature of that role and its relation to species and speciation. The recent boom in philosophy of biology (in part caused, in part signalled, by Sober [1984]) began with the attempt to understand and resolve these controversies. They are central to this work, too.

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Views about selection have tended to cluster into two camps; I will tententiously call these the American and the British tendencies. The Americans have tended to suppose:

1. The most central phenomenon evolutionary biology must explain is diversity and constraints on diversity.
2. Selection is important, but the evolutionary trajectory of populations is affected by much more than within-population natural selection.
3. When selection acts, it typically acts on individual organisms. Individual organisms within a population are more or less fit. Those fitness differences may not result in differential reproduction (for actual fitness can vary from expected fitness), still less to an evolutionary change in the population as a whole. But the primary bearers of fitness differences are individual organisms.
4. Theorists within this group are often pluralists. That is, they think that while the usual bearers of fitness properties are organisms, they are not the only biological individuals who are more or less fit. Groups of organisms, and even species, are potentially units of selection. In special circumstances even individual genes are units of selection. In particular, this is true of so-called outlaw genes; genes that improve their own chance of replication at the expense of the organisms in which they reside. Such a gene, according to this tendency, really is a unit of selection. But these genes are the exception rather than the rule.
5. The American school is typically sceptical of attempts to apply evolutionary theory to humans. They do not suppose that there is an “in-principle” problem in studying human evolution. For the members of this tendency agree that we came into existence as a standard product of evolution. But they are sceptical of actual attempts to apply evolutionary theory to human social behaviour; in particular they are sceptical of sociobiology and its intellectual descendants.

Paradigm Americans are Lewontin, Gould, Levins, Sober, and Lloyd (oddly enough, all Americans). In the British tendency, we find exemplified the following ideas:

1. The fit between organisms and environment – adaptedness or good design – is the central problem evolutionary biology must explain.
2. Consequently, though the British tendency does not deny the importance of historical, developmental and chance factors in deter-

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mining the evolutionary trajectories of populations, natural selection plays a uniquely important role in evolutionary explanation.

3. In some fundamental sense to be explained, the gene is the real unit of selection. This is true not just in the exotic case of sex ratio genes and other outlaws, but in the routine cases as well. For example, a gene that improves the camouflage pattern of a bittern is no outlaw. In improving its own replication prospects, it improves those of all other genes in the genome. But it, rather than the bittern itself, is the real unit of selection.
4. This group is sceptical about “higher order selection”; they doubt that groups of organisms or species form units subject to selection and evolution within competing metapopulations.
5. Members of this group endorse the application of evolutionary theory to human social behaviour, not just in theory but in practice.

Paradigms within the British tendency are Williams, Maynard Smith, Dawkins, Dennett, and Cronin (by no means all British). Indeed, my characterisation of these groups is tendentious, not just in the pseudo-national labels but also in suppressing the fact that these thinkers are less uniform and more finessed in their conceptions of evolution than my ideal typology suggests. But even so, there is a real clustering in positions, and one message of this collection is that this clustering is due to historical accident rather than a necessary connection between these theses. In my view:

1. Both adaptation and diversity are real phenomena of great significance. Both need to be explained. No-one disagrees explicitly with this claim, but in practice evolutionary theories tend to focus on one phenomenon or the other.
2. Natural selection does play a unique role within evolutionary history, a role that must be recognised by evolutionary theory. But selection does not, in general, consist in the adaptation of organisms to their environments.
3. There is an important sense in which genes are the units of selection. But so are other gene-like replicators. Moreover, the pluralists are also right to insist that groups and species sometimes play a role in evolution strikingly like that played by organisms. The members of the British tendency are usually willing to admit the in-principle possibility of such phenomena, but they have been notably unwilling to countenance their actual existence.

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4. American caution about the application of evolutionary theory to human behaviour is well-founded. But I will try to show by actual example the virtues of an evolutionary perspective on cognitive phenomena.

The next six chapters in this collection explore general themes within evolutionary theory, themes that reappear in a more concrete setting in the final five chapters on the evolution of cognition.

II THE UNITS OF SELECTION REVISITED; OR WHATEVER HAPPENED TO GENE SELECTION?

Famously, G. C. Williams and Richard Dawkins have argued that the unit of selection is the gene: The history of life is the history of more or less successful gene lineages. On this view, it's a mistake to suppose that organisms are the units of selection. The critical consideration is that evolutionary change depends on cumulative selection. So the units of selection must persist: they must face the tribunal of experience repeatedly, not just once. Organisms are temporary beings; here today; gone tomorrow. They reproduce but are not copied. That is obviously so (the idea runs) in the case of sexual organisms. For no offspring's genome is identical to that of any parent. But asexual reproduction is not copying either. As Dawkins points out, an adventitious change to the phenotype of an asexual organism is not transmitted to its descendants (Dawkins 1982, pp. 97–8). Gene tokens are equally impermanent. But genes, unlike organisms, are copied. Gene lineages – chains of identical gene tokens – are around both today and tomorrow, to repeatedly experience selection's whip.

So when we think of the tree of life, we should think not so much of organisms as gene lineages. Since organisms cannot be copied, they cannot form chains in which each link is a copy of the one before it. But since genes can be copied, they can form lineages; chains of copies, with each link being a copy of its predecessor. The gene's-eye view of evolution takes over the notion of competition, but applies it to competing gene lineages. For lineages can sometimes be many copy-generations deep and they can vary in bushiness, too. A gene may be copied many times, and the copies may form an increasingly broad lineage as well as a deep one. Alternatively, a gene lineage may be thin,

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with only a few copies existing at each generation. Differences in copy number are usually not accidental, so genes have properties that influence their propensity to be replicated. These properties are targets of selection. Furthermore, since genes are replicated via the reproductive success of organisms, success for one lineage has implications for others. The life or death of an organism has its evolutionary consequences indirectly, by influencing the copying success of the genes within it. Well-built organisms mediate more effective replication of the genes within them. Selection acts through organisms to target some genes rather than others.

This whole conception has been extremely controversial. But some order was injected into this debate through the replicator/interactor distinction (Hull 1981).¹ Obviously, it would be mad to deny that organisms play some especially significant role in evolutionary processes. Gene selectionists have tried to accommodate this obvious truth by distinguishing two different roles in evolution. Replicators transmit similarity across the generations, and interactors interact with the environment with varying success, hence biasing the transmission of replicators. For replicators help construct those interactors, and hence replicators that construct successful, well-adapted interactors do better than those implicated in the construction of less successful ones. Organisms, naturally, are paradigm interactors. In finding a role for organisms, the replicator/interactor distinction resolved some of the problems in the gene selection debate. But very tough questions remain.

First, there is a threat of triviality. Once gene selectionists develop the replicator/interactor distinction, it may be that their theory merely renames the familiar distinction between genotypes and phenotypes. Can gene selectionists stake out some distinctive territory while still recognising the complexity and indirectness of gene's causal actions in the world? Second, gene selection ultimately depends (or so I will argue) on the informational conception of the genome; a conception which has recently come under sustained criticism. Third, it is one thing to develop and defend a distinction between replication and interaction; it is another to show that the genes are the replicators, and organisms the interactors. Replicator selection may not be gene selection, and organisms may not be the only interactors. Let me sketch these ideas a little more fully, and indicate the places I take them up later in this collection.

*Overview**Is Gene Selection a Genuine
Alternative to the Standard View?*

Once gene selectionism comes to rely on the replicator/interactor distinction, perhaps that view just renames the elephant, for the genotype/phenotype distinction is standard fare in evolutionary biology. So, too, is the assignment of fitness values to individual gene types by calculating the average fitness of the bearers of an allele in a population. Calculating gene fitness is a standard way of tracking or representing evolutionary change. So much so, that evolution itself has occasionally been defined as change in gene frequency. How does gene selection, shorn of its metaphors, differ from this banal conception of evolution? Elliot Sober, in particular, has pressed this objection. In his view, gene selectionists face a dilemma: They are pushed either into empirically unsupportable views about the nature of the genotype/phenotype relation or into a view that is nothing more than a restatement of the received conception (Sober 1993).

I argue in Chapter 2 and Chapter 3 that this very deflationary view of gene selection would be a mistake, for it overlooks the significance of Dawkins' ideas about extended phenotypes. Genes have phenotypic effects that influence their replication propensities. If those effects were almost always effects on the design of the organisms carrying the gene, gene selection would rename the phenotype/genotype distinction. But some genes have short arms, and others have long ones. Outlaws typically have short arms. For example, the critical effect of a segregation distorting gene is on its rival allele. The existence of outlaw genes is not controversial; neither is the idea that they are genuine cases of gene selection. It is worth remarking, though, that this concession is less innocent than critics of gene selection suppose. One standard argument against gene selection is that genotype/phenotype relations are too variable and indirect for genes to be "visible" to selection via their phenotypic effects. But it is very hard to claim that *only* outlaw genes are selected in virtue of their fitness properties, for what are they fitter than, in virtue of their being outlaws? Presumably, the normal, cooperating, phenotype-building genes. But if we can think of these ordinary genes as being "visible" to selection (and selected against) in the presence of outlaws, it is hard to see how they could cease to be visible when there are no outlaws. Arguments against gene selection that depend on the complexity and indirectness of the effects of genes on

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phenotypes threaten to unravel, once the example of outlaws is conceded to gene selection.²

The existence of long-armed genes – genes with extended phenotypes – is more controversial. But if Dawkins is right, they are more widespread. There is a parasitic barnacle from the *Rhizocephala* group that chemically castrates and feminises her host, a crab. The genes responsible for that effect replicate in virtue of effects outside the body of the parasite. These genes are not outlaws. They promote the replication of every gene in the parasite genome. But their critical adaptive upshot is not a feature of the parasite's body. Outlaws may be exceptional. But extended phenotype effects are widespread in nature. Parasites themselves are exceptionally numerous, and virtually all carry genes that manipulate hosts and/or suppress their defences. Moreover, many other organisms – organisms whose way of life is not parasitic – carry manipulation genes. As Krebs and Dawkins point out, much animal signalling is an attempt at manipulation (Krebs and Dawkins 1984). Furthermore, mounds, nests, tunnels, casings and the like are adapted structures but are not part of the phenotype of individual organisms. Their adaptations, too, are the result of extended phenotypic effects. Gene selection, then, directs our attention not just to outlaws but to these effects; important evolutionary phenomena we might easily overlook if the standard model were our conception of evolution. It is no mere relabelling of the genotype/phenotype distinction.

The Informational Gene

Why suppose genes form lineages of copies, whereas organisms do not? It is true, of course, that while organisms resemble their parents in many respects, there are differences as well. In particular, the genotype of those organisms formed through sexual reproduction will be like that of neither parent (though, of course, a defence of gene selection must show rather than presuppose the special significance of gene similarities). So perhaps the critical difference is fidelity. When a gene is copied, normally the copy is exactly the same as the template, and that is never true of reproduction. But that idea leads to problems. When all goes well, gene replication does produce new genes that share their antecedent's base sequences. But the route from base sequence to phenotypic effect is complex, indirect and many-many, for in different cellular contexts the same base sequence can yield a different effect,

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and vice versa. Hence, the biologically relevant properties of a gene token include much more than its base sequence. The surrounding genes and other aspects of the cellular context will play a role in determining whether and how a sequence is transcribed. Hence, organism lineages cannot clearly be distinguished from gene lineages on grounds of copy fidelity.

In my view, the informational conception of the genome is one foundation for the view that gene lineages have a special status. An organism's genome (on this view) is a set of instructions for making that organism. Gene copying is the ground of reproduction, for it's the mechanism through which the instructions for making organisms are transmitted over time. This view is very widely expressed. Here is one recent instance:

How is it . . . that an egg develops into a mouse, or an elephant or a fruitfly, according to the species that produced it? The short answer is that each egg contains, in its genes, a set of instructions for making the appropriate adult. Of course the egg must be in a suitable environment, and there are structures in the egg needed to interpret the genetic instructions, but it is the information contained in the genes that specifies the adult form. (Maynard Smith and Szathmary 1999, p. 2)

If this view of genes and the genome could be supported, it really would vindicate gene selection. It would suggest that, most fundamentally, evolution is a change in the instruction set. But to put it mildly, this idea is controversial. In particular, Developmental Systems Theorists argue that there is no sense in which only genes carry information about phenotypes. In their view, the only theoretically innocent view of information is covariation. It is true that if we hold the rest of the causal context constant, particular alleles covary with phenotypic outcomes. But that is true of other developmental resources. For example, many reptiles have temperature dependent sex determination. So for them, a particular incubation temperature, holding other factors constant, covaries with a particular sex. So by the same logic, we should say that a particular temperature codes for, programs, or carries the information that the crocodile is female. Developmental Systems Theorists regard this as a *reductio* of informational conceptions of the role of the gene in evolution.