

The Parasitic Host: Symbiosis *contra* Neo-Darwinism

MICHELLE SPEIDEL

Introduction

Darwinism, and its modern formulation, neo-Darwinism, have often been the target of philosophically motivated attacks which centre on what are often seen as the ideological underpinnings, assumptions or consequences that are believed to emanate from Darwinism's Malthusian origins. More often than not, these attacks focus on the 'improper' extensions of Darwinism into the social realm, in the areas of social engineering, evolutionary psychology (or its much-derided former incarnation, sociobiology), biopolitics, and the like. Occasionally, some attacks on Darwinism and neo-Darwinism have a force that is more 'scientific' in nature, that is, the attacks on the ideology attempt to show the entailment of real consequences for the methodology and practice of biological science itself, and are serious challenges not just to the ideological aspects of Darwinism, but to the theory itself. The group of approaches to evolution that can be grouped under the heading of 'symbiosis' appear to be challenges of precisely this kind.

Symbiosis, the phenomenon that describes the 'coevolution' of two distinct species into a partnership-oriented evolutionary relationship, does appear at first glance to be absent from most descriptions of neo-Darwinism as a scientific theory, since such descriptions invariably prescribe competition as the primary impetus for evolutionary change. As I hope to show, there is a real sense in which a theory which emphasises competition cannot explain cooperative behaviours, except by fairly circuitous reroutings of the operational terms of the theory. Furthermore, I will argue that the real strength of symbiosis as a challenge to neo-

Darwinism lies in the very notion of symbiosis itself, quite apart from the 'cooperative' nature of symbiotic associations.

Symbiosis as a mode of organisation of living things in an evolutionary context has serious consequences for neo-Darwinism as a theory in terms of its ability to describe, or more strongly, *explain* evolutionary change. This, as I will show in this paper, is why symbiosis should not be ignored as a challenge to neo-Darwinism. Symbiosis-based approaches, even if taken merely as descriptions of evolution which contain 'cooperative' modes of behaviour are themselves fairly important in that they show in dramatic relief the shortcomings of neo-Darwinism. But if symbiosis is taken seriously as an *alternative* mode of organisation of living things, it has very strong consequences indeed for the conceptual apparatus of neo-Darwinism.

The following discussion will outline the historical evolution of symbiosis as a conceptual dissent to neo-Darwinism. One theme that is present in the history of symbiosis is the persistent attempt to deal with anomalous symbiotic phenomena by acknowledging their existence, but also treating them as specific adaptations in special isolated cases. Such closely integrated cooperation is seen as the exception, rather than the rule in nature.

Yet Lynn Margulis has claimed that the prevalence of such symbiotic associations in nature clearly calls for a new model of evolution, one that would be inconsistent with conservative neo-Darwinism. Margulis believes that symbiosis is the rule in nature, rather than the exception. She attacks neo-Darwinism for its assumption that evolution is a competitive process. Once the core assumptions of neo-Darwinism and historical background of symbiosis have been examined, it will be possible to discuss this claim in more detail. Precisely how symbiosis effects evolutionary theory can then be outlined.

To this end I will first discuss what I take to be the core elements of neo-Darwinism, and look at some limits placed upon the application these elements to biological entities. Then a look at the historical development of symbiosis with reference to some examples of symbiotic systems will allow a description of what sorts of problems symbiosis may cause for neo-Darwinism. Certain approaches to symbiosis that come from within the neo-Darwinist research programme will also be outlined.

I will argue that first, the interaction of the components of neo-Darwinism forces evolutionary theory to view biological entities as decomposable and separable from their environment, and symbiosis

problematises this type of delineation. Second, I will argue that neo-Darwinism's presumption of decomposability also compels one to adopt the view that nature is essentially competitive, and that this view makes any cooperative behaviours explainable only with reference to individual fitness. Again, symbiosis makes this account of living systems untenable.

Core Elements of Neo-Darwinism

I characterise neo-Darwinism as having three core components: natural selection, variation and heredity. These elements are the base-line necessity for any naturalistic theory (as opposed to an argument by design) of evolving entities. Darwin's insight was to propose the interaction of these elements as an alternative explanation for the adaptedness of living things to that of a creationist explanation. Yet it is often stated that evolution needs only natural selection and variation, in the sense of differential selection of variants, in order for evolution to occur. However, if this were true, evolution could never be cumulative and adaptive. Without a hereditary mechanism of some kind, evolution could never get off the ground in the first place, it would lead to constantly shifting, disorganised change. The interaction of these three elements of natural selection, variation and heredity, and the resultant interpretation of these interactions lead to certain constraints upon the way evolution is supposed to occur.

Natural selection describes the differential survival rate of a number of organisms. Darwin, famously inspired by Malthus, designated natural selection as a mechanism whereby only a few offspring of a given species would survive, due to competition for limited resources. It is important to remember that natural selection can be conceived of as a purely negative force. It does not so much 'select' individuals for survival (although this kind of language is often used) as cull individual organisms. The organisms that are 'selected' by the action of natural selection are simply those which are not unfit. Yet because of its Malthusian origins, 'natural selection' in Darwin's sense is interpreted as entailing that life is essentially competitive, whereby each organism, vying for resources, is interested only in surviving. This can be revised to the claim that organisms are interested in survival insofar as they live only to reproduce and leave offspring, and the 'fitness' of an organism is to be measured with reference to this. Such teleological language is often found in neo-Darwinism, but

neo-Darwinism itself claims to be non-teleological. The trend today is to use the term 'teleonomy' instead¹, to denote systems that 'act as if' they are goal-directed.² At any rate, natural selection should be understood as undirected in the sense that it is a contingent matter what new organisms are produced, and thus the operation is non-teleological.

An important aspect of the concept of natural selection is its relationship to the 'environment'. Properly speaking, natural selection operates when a group of individuals compete for limited resources in an environment. The environment, with its limited resources as the constraints that allow natural selection to operate, determines which organisms will survive. As Elliot Sober puts it in his textbook on the philosophy of biology, "The...properties of an organism and the environment it inhabits determine how fit that organism is."³ Hence it is clear that any description of fitness or adaptation must be made with reference to the environment.

The second component in a theory of evolution by natural selection is variation. Variation is the mechanism which provides the 'raw material' for natural selection to work upon. Variation is randomly generated in the sense that it is undirected and uncorrelated with selection pressures. An organism does not recognise actual selection pressures and produce favourable variations in response, as is supposed by Lamarckian inheritance. Rather, undirected variation is acted upon by the natural selection. Any number of different variants are produced, but only a few survive. The accumulation of random variations through the action of natural selection is the end result of evolution.

Heredity is the third component of evolutionary theory, and it ensures that evolution is conservative and cumulative. Earlier in this century many biologists still believed that selection pressures in the environment could actively induce corresponding changes in the hereditary material of the organism, after Jean-Baptiste Lamarck's hypothesis of 'inheritance of acquired characteristics.' However, the Lamarckian question as to whether variation could occur as active evolution toward a given environment was later answered in the negative by the work of August Weismann, and this answer determined the present interpretation of heredity of neo-Darwinism as a theory today.

¹ The term comes from Monod, Jaques, *Chance and Necessity*, (Collins Fontana Books: London 1974)

² There is, of course, a sense in which goal-directed systems need not be interpreted as necessitating a designer; rather, one can use the terminology of "goal-directedness" to indicate a property of the system itself, rather than a design intention.

³ Sober, Elliot. *Philosophy of Biology* (Oxford University Press 1993) p.73

Weismann's work showed that the environment directly affected the body of the organism, but could only indirectly affect its genetic material. He showed that in each organism's early development, the hereditary material was partitioned off sufficiently early in development as to preclude the possibility that any changes in the organism could directly be retranscribed onto the hereditary material. This partitioning became known as the 'Weismann Barrier'. Thus the genes directly affected the growth of the individual organism, but the development of the organism could not affect the hereditary material of the cell in return. The discovery of the unidirectional flow of information in DNA replication and translation also ensured that the organism could never actively change itself in response to environmental pressures. It also reinforced the idea that there was a unidirectional vector of information between the organism and the environment; there was no possibility of informational feedback from the environment to the organism, rather, the environment determined which organisms were unfit by selecting against them. Thus the Weismann Barrier made certain that the genome was a functional conserved unity, and the unidirectional flow of information confirmed that the genome was quite separate from the externalised environment.

The interaction of these three core elements of neo-Darwinism leads to certain conclusions about how 'entities' in evolutionary terms are supposed to function. Natural selection must 'act on' some entity--this is usually characterised as the organism itself. After all, the organism is what lives or dies, and hence it is natural to think of the organism as the locus for evolutionary change. However, Richard Dawkins' notion of the "Extended Phenotype" showed that 'the organism' was in fact an arbitrary category, at least insofar as the organism is taken as the set of phenotypic characteristics determined by one complete genotype.⁴ A consequence of his position is that genes in one organism can have phenotypic effects in other unrelated organisms. For instance, perhaps it could be said that the genes that determine an organism's colour may affect the ability of other organisms which prey upon it to discriminate that colour effectively. The ability to discriminate the color would be in the phenotype of a different organism than the original genotype itself. Since in this sense there are no clearly delimited organisms, Dawkins believed that the gene could be seen as the entity that natural selection 'acts on'.

⁴ The **genotype** is the set of genetic instructions or genetic material in an organism, the **phenotype** is the set of outwardly manifested characteristics in the organism, such as colour, size, behaviours, etc.

This debate over the locus of natural selection, is commonly known as the 'unit of selection debate' and it is a strong theme in the philosophy of biology. The reason for this is that the three elements of the theory of evolution by natural selection (natural selection, variation and heredity) do not themselves give any clues as to the types of entities that natural selection acts upon. All that is required is that natural selection acts upon some thing, and whatever this thing is, it is in principle identifiable and separable from any other non-salient features of the evolving system. It is, after all, held to be that thing which is selected, as opposed to the environment, which is doing the selecting.

The unit of selection is thus a necessary feature of evolution by natural selection. It is held to be many different things by different neo-Darwinists, but is most commonly seen as the organism. Some see it as the gene, a few still maintain that it can be a group of related organisms, such as a species. I will argue that symbiosis causes problems for neo-Darwinism in that whatever the unit of selection is held to be, it will not be easily distinguishable or identifiable in a close symbiotic relationship. I now turn to an outline of the history of symbiosis, culminating in Lynn Margulis' work on endosymbiosis. This will allow some examples of symbiosis to be examined, as well as show how they relate to biological entities.

Historical Evolution of Symbiosis

Jan Sapp sees the development of symbiosis as a parallel track in the development of Darwinism in biology, yet he also sees it as a dissenting footnote to Darwinism. He finds little mention of symbiosis in literature on theoretical biology; it seems that it is also absent in anti-Darwinian neo-Lamarckian literature. It is even absent in literature on ecology, which seems odd given that ecology is perhaps the biological discipline most able to accommodate mechanisms involving cooperation. The precise relationship between Darwinism and symbiosis is difficult to define in historical terms for this reason. Yet it may be possible to define their relationship by showing how each looks upon the problems of evolution: the production of novelty, and the role of selection.

The first symbiotic relationships discovered in nature were those of the lichens, which are all associations of a fungus and an alga. In 1868, Simon Schwenderer, a Swiss botanist, first proposed that lichens, which had previously been inimical to Linnaean classification, were in fact two types

of organisms locked in what he termed a “master-slave” relationship. His “dual hypothesis” as he called it, was not accepted fully until around 1900. Some of those who did accept the dual hypothesis were unhappy with Schwenderer’s assertion that the relationship was a “master-slave” relation. There was disagreement among botanists who worked with lichens over the degree of parasitism in these relationships. Some saw the master-slave metaphor as too politicised, and replaced it with a terminology based on parasitism. Yet others saw the relation as more cooperative, and complained that the terminology based on parasitism carried too many connotations of disease and plague. In 1877, Albert Bernhard Frank, one of the first botanists to accept the dual hypothesis, proposed the introduction of a neutral term that did not presuppose any degree of parasitism and only described the co-existence of two species in or on one another: he recommended the term symbiosis.⁵ The introduction of this scientific term did not, however, stop the debates over the degree of parasitism in such relationships. Pierre Van Beneden had earlier proposed the term “mutualism” to describe the same types of relationships. He believed that there was a continuum of relationships in nature from the “parasite” at one end of the continuum to the “free animal” at the other, with various degrees of mutual or symbiotic relationships falling in between.⁶ Mutualism eventually came to be used to describe cooperative behaviour between and among separate, relatively unrelated, species.

This early history of the term symbiosis has caused some difficulties in the usage of the term today. There has been a tendency to use the terms mutualism, cooperation and symbiosis interchangeably. Margulis has argued that the term symbiosis should be reserved for designating relationships between organisms of different species. Furthermore, she believes that approaches which fail to make this important distinction are wholly inappropriate to dealing with symbiosis in its most important form. This will become important later when we examine some neo-Darwinist approaches to cooperative behaviour.

Over time, botanists began to see more and more evidence of symbiotic associations in nature, ranging from complex plant and animal associations down to symbiotic associations between bacteria and viruses. However, in the late nineteenth century, researchers began to believe that the secrets of

⁵ The coinage of the term is usually attributed to Anton de Bary, yet he did not himself use the term until 1879. Sapp, Jan. *Evolution by Association: A History of Symbiosis* (Oxford University Press 1994) pp. 4-6

⁶ Sapp, p.8

all life could be found by understanding the cell. It had already been discovered that all cells came from other cells, and that plant and animal cells were very similar in function and organisation. Thus, it was thought that research into the cell would shed light on all the functions of the higher organism. The single cell was generally thought of as an individual, self-sufficient organism, but the discovery of more and more organelles, or separate specialised structures within the single cell, led many to adopt explanatory metaphors using phrases such as “division of labour” and “cell-state” or cell-republic”.⁷ The tendency was, therefore, to treat the individual cell as prior to any enquiry concerning the specialised functioning structures within it.

There were, however, some researchers who wanted to treat individual cells as cooperative entities. Richard Altmann, in the late 1880’s, suggested that the cell evolved through the conglomeration of bodies he called “bioblasts” into a collective colony. He believed that these bioblasts, which seemed to be present in all animal cells, were responsible for all cell metabolic activities. Altmann’s work was severely criticised, but the existence of bioblasts was later supported by the work of Alexander Benda in 1897; these bioblasts were what we today call mitochondria. Altmann’s theory of cell evolution was largely ignored. The development of theories for the evolution of the cell was soon eclipsed by the discovery of the importance of the nucleus as the carrier of genetic information. Weismann’s work on this subject continued to gain support, and soon it was believed that the nucleus, as well as being the receptacle for genetic material, was itself responsible for the differentiation of cell organelles and their functions.

‘Nucleocentrism’ as a research program came to dominate many fields of biology, and still continues to do so. The assumptions behind this program are related to what has already been said about the nature of heredity and variation: one, that the nucleus contains the genetic material; two, that this material is the source of development for the differentiation within cells and the maintenance of their metabolic functions; three, that this genetic material is that which is passed between generations as heritable material, four, that genetic variability is gained through random changes and reshuffling of this material alone, and finally that this genetic material is self-contained and separated off from the external environment.

The discovery of DNA as the carrier of hereditary information merely continued this trend in a different guise: the DNA was seen to be the

⁷ Sapp, pp. 35-39

‘program’ that the cell carried out, and was responsible for all cell functions, as well as all higher functions of the larger organism. Research into the evolution of cells themselves was generally pushed aside by this research program. Since it was believed that the nucleus or DNA was the ‘program instructions for life’ it was left to researchers to discover its origin, and the evolution of the cell would presumably be secondary to this.⁸

However, the emphasis on researching the ‘universal code’ of DNA and RNA also disclosed some interesting findings in the field of symbiosis. The discovery of bacterial genomes, as well as the discovery of viruses as “naked genes” led to research into the mechanisms by which these genes interacted with each other. Since it was known that viruses and bacteria were responsible for many illnesses, the research was driven by an attempt to understand the nature of pathology. The discovery of such extra-cellular genetic particles was itself shocking to investigators, who had previously relied entirely on a Weismannian model of inheritance where genetic material was separated off from the environment by the nucleus.

The Problem of Separating the Organism and Environment: Extra-cellular Genes

Soon it began to be recognised that extra-cellular genetic particles, such as viruses, could alter the genome of other cells by being incorporated into them. Research seemed to show that this process was almost always fatal to the host cell, and viruses were generally seen as worse than parasites, as harmful pathogens.

Joshua Lederberg’s work in the 1940’s began to show that the ‘host – parasite’ or ‘pathological’ picture of the virus-bacteria relationship was much more complex. He showed that viral DNA, once injected into its host, could be incorporated into the bacterial host’s DNA as a harmless segment of DNA, called a prophage, which would then replicate along with the bacterium’s own genetic material. The prophage seemed to confer resistance to infection from other external factors onto the bacterial host. Such prophages could stay inside cells for many generations, either staying inert and allowing the bacteria to do their replication for them, or else later

⁸ This research program is still very much alive, and the Miller-Urey experiments in the 1970’s to construct a “primeval soup”, as well as the work of Cairns-Smith and those working on the “RNA-world” theory attest to this.

become activated and kill their host, and be released to infect other bacteria.

Lederberg realised that the relationship was hard to define; it seemed to be a host-parasite relationship since the viruses were using their bacterial hosts for replication. But on the other hand it could also be seen as a close symbiotic relationship, one which the infection-resistant host could not do without. He also realised that the difficulty of adequately defining such a relationship led to a larger problem having to do with the nature of the organism: how could one designate the 'normal' components of a cell when external supposedly 'pathological' factors were so closely integrated in a cell's normal functioning?⁹ Above it was noted that the organism and the environment are supposed to be separable in some way, and the genetic material is also a separate functioning entity. Lederberg's work cast doubt on this constraint of neo-Darwinism, since it became increasingly difficult to delineate the internal from the external in such gene-swapping situations. Lederberg even realised that prophages were an important source of genetic variation among bacteria, "a special form of sexuality"¹⁰.

Lederberg's work and the continuing research into the functioning of bacteria and viruses make two things clear. First, the cell's own genome is not necessarily strongly causally related to the functioning of the cell. Extra-cellular genomic factors can be implicated in normal cellular function. Second, the organism and the environment are not separable in principle if it is the case that environmental extra-cellular factors exert such a powerful force on the functioning organism. A host-parasite description of a relationship is only available when it is possible to delineate the partners in the relationship, and show that parasite impedes the normal functioning of the host in some way. In the bacteria-viral relationship described above the supposedly parasitic virus gives a benefit to the host bacterium through the conferral of infection resistance. And since the virus can also be seen as a source of genetic variability, this also may be included in the normal functioning of one or both of the partners. The host-parasite relationship is not clearly definable for this reason. The relationship must rather be described as symbiotic.

The architects of the Neo-Darwinist synthesis did not give these early investigations of symbiosis much credence. The development of cell theory as well as the development of research into bacteria and viruses was still

⁹ Sapp, pp.158-161

¹⁰ Sapp, p.160

overshadowed by the nucleocentric research program. But the restrictive scope of this research program was not the only problem facing researchers into symbiosis. In fact, the growth of knowledge in the areas of bacterial DNA as well as cell theory in general became the basis of perhaps the most important development in symbiosis: Serial Endosymbiosis Theory.

SET

Lynn Margulis's serial endosymbiosis theory, or SET, now widely accepted by the scientific community, theorises that in fact all complex nucleated cells (eukaryotes) evolved as communities of interacting free-living bacteria (prokaryotes), which themselves already had the ability to fulfil the functions that the eukaryotic organelles now fulfil. For instance, mitochondria, the energy producing organelles in animal cells, are thought to have been bacteria that had already developed an efficient oxygen-respiring ability, which were later incorporated into a cell host which provided protection against acidity and high temperatures. Thus, it is believed that eukaryotes, the basis of most complex plant and animal life on earth, were formed only through a mutually dependent relationship between various types of bacteria.¹¹ This conclusion is in some ways very similar to Richard Altmann's cooperative theory of cell evolution mentioned earlier.

Margulis also discovered homologous structures in the centriole and basal bodies (to which flagella and cilia, (motility organelles) are attached) in both prokaryotes and eukaryotes. She interpreted the existence of these homologous structures as further evidence for SET. Margulis' work took years to be accepted, since it was thought that the homologous equivalents she discovered were not in themselves enough evidence to support SET. The reasons for this actually had to do with Neo-Darwinism's conception of how and at what pace evolution occurs.

The neo-Darwinist synthesis, with its insistence on genetic change through random reshuffling of genetic material acted upon by natural selection, was interpreted as suggesting that evolution could only happen slowly and very gradually. Opponents of the SET insisted that eukaryotes could only have evolved gradually from prokaryotic ancestors. Gradualist

¹¹ Margulis, Lynn. *Symbiosis and Cell Evolution: Microbial Communities in the Archean and Proterozoic Forms*, 2nd Ed. (New York:1993) p.2ff

detractors of endosymbiosis expected to see a slow, gradual accumulation of adaptations rather than a series of endosymbiotic events. Though some agreed that SET was “aesthetically pleasing”¹² they believed there must be a ‘missing link’ as yet undiscovered, that would show the gradual transformation of prokaryote to eukaryote. Yet Margulis’ description of the evolution of eukaryotes is now an established scientific theory.

Symbiosis is seen as the end result of a previously parasitic relationship only by an approach that sees evolution in terms of the gradual accumulation of adaptations, and symbiosis will be seen as the exception rather than the rule by such an approach. Such an approach would have to depend entirely on some means of individuating the organism, in order to determine the entities ‘host’ and ‘parasite’. However, if one treats what are normally designated as host-parasite relationships as symbiotic wholes, given that the endosymbiotic origin of life shows that it is difficult to designate ‘the organism’, it should be clear that the neo-Darwinist assumption that the organism and environment, host and parasite, are separable is placed in doubt. The organism as a unity is in fact a symbiotic complex in its own right.

To return to the debate about the ‘unit of selection’, we can see that if even a single cell is in fact a cooperative colony of a sort, it is difficult to designate exactly what the ‘unit of selection’ is in such a evolutionary situation. If we agree with Dawkins, and hold that the gene is the unit of selection, it is worth remembering that mitochondria, the organelles in the cell which provide energy, have their own genetic material, distinct from that in the nucleus of the cell. Which genetic material is ‘acted upon’ by natural selection in this type of evolutionary situation? Yet if we take the standard line and treat the individual as the unit of selection, we must admit that the individual cell as a collective complex makes this position problematic.

Problem of Cooperation when Competition is Assumed

Margulis’ work on SET has shown that the distinction in principle between organism and environment is violated by symbiosis. Margulis also claims that symbiosis represents a challenge to neo-Darwinism in that neo-Darwinism, with its insistence on competition, tends to see cooperation as the exception, rather than the rule. She objects to the fact that competition

¹² Sapp, p. 161

is built into any models of evolution that use the population biology approach, which views all evolutionary changes as changes in gene frequency:

In these mathematic machinations of evolution, the number of individuals in a population or a species is taken as the basic measure. The usual interactions that are explored between individuals (or species) are competition (for resources, space, etc.) and predation...The incorporation of “cost-benefit analysis” methods borrowed from insurance practices has led to the biologically puerile numerology that systematically ignores chemistry, biochemistry, molecular biology, and geology. Nevertheless such aseptic language dominates current evolutionary theory.¹³

Apart from the issues raised about the applicability of certain mathematical tools in evolutionary theory, this remark actually points to two other difficulties. First, the fact that competition is built into models of evolution, and second, the fact that individuals are the basic measure. We will investigate these difficulties by looking at the type of approaches that Margulis is presumably uncomfortable with: the group of approaches which seeks to explain altruism.

One group of general approaches to symbiosis can be roughly grouped under the heading of altruism. Altruism, in its broadest form, is the exhibition of a type of behaviour that increases another's fitness at the expense of one's own. It is thought to run counter to Darwinism since any behaviour that reduces fitness is maladaptive and hence should be selected against in the long run. Thus the research programme that deals with altruism seeks to explain how such cooperation can be explained given the assumption that nature is essentially competitive in the neo-Darwinist paradigm. This research programme broadly includes such terms as reciprocal altruism, altruism, group-selection, kin selection, and evolutionary game theory. Each term will be explained in context in this section.

Reciprocal altruism, a thesis proposed by Robert Trivers in 1971, claimed that natural selection operated in a way such that acts of kindness would be recognised and repaid in kind later on, so that ‘altruistic’ acts

¹³ Margulis, Lynn “Symbiogenesis and Symbioticism” in *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis* eds. Lynn Margulis and Rene Fester (MIT Press 1991) p.6

were actually selected for by natural selection. Trivers specifically invoked the concept of symbiosis as an adjunct to his theory: "Reciprocal altruism can also be viewed as a symbiosis, each partner helping the other while he helps himself."¹⁴ V.C. Wynne-Edwards proposed the group-selection hypothesis, which caused controversy by claiming that this type of cooperation could be explained by the possibility that evolution could work at the level of the group of individuals as a whole, rather than at the mere level of individual organisms, thus suggesting that the group could be seen as the 'unit of selection'. It was claimed that 'cooperative' strategies enlisted by species as a whole would be adaptive for the continuance of that species on an evolutionary level.

However, the thesis of group selection has been discredited and explanations of altruism have been replaced with explanations that are based on the idea that the unit of selection is either the gene or the individual. Maynard Smith, in his own attack on group selectionism, pointed out that cooperation is an unstable strategy; introduce a competitive element into a cooperative group and the competitors will soon take over the cooperators. For this reason, altruism at the intraspecies level ought to be explainable by Hamilton's famous kin selection hypothesis. In the kin selection approach it is claimed that if evolution occurs at the level of the genotype, then any strategy that maximises the number of genes passed on will be an adaptive strategy. Strategies that do this may appear to take the form of altruism since parents will care for any members of the group which carry some of the parental genes into the next generation. The idea is that an individual's own fitness will be sacrificed to ensure that its offspring will be increased. On this approach, as J.B.S. Haldane remarked, one would be prepared to give up one's life for exactly two brothers, or eight cousins.¹⁵ However, it seems that any kin selection hypothesis must have some kind of kin recognition system in order for it to work, since there must be some way for members of a species to identify related members so that they can protect them. Thus the reciprocal altruism and kin selection approaches, by assuming competition as the rule, must also account for the generation of recognition in order to explain cooperation.

¹⁴ Trivers, Robert. "The Evolution of Reciprocal Altruism" *Quarterly Review of Biology* 46 (1971) as quoted in Sapp p.199

¹⁵ Maynard Smith, John. *Did Darwin Get it Right: Essays on Games, Sex and Evolution*, Penguin 1989 p.187

A related area of discussion of symbiosis which is closely related to kin selection and reciprocal altruism has its origins in game theory. It also is concerned to explain how cooperative strategies arise in an essentially competitive world. Maynard Smith is credited with introducing game theory to the domain of biology, by using classical game theory to disclose evolutionary stable strategies (ESS). This approach was designed to answer his own objection mentioned earlier, namely, that a cooperative system was highly invadable by competitive elements, and was thus not a stable strategy. Evolutionary game theory was devised to show how it was that cooperation could be shown to be a stable strategy. However, the results actually showed that cooperation and competition were equally stable strategies.

Evolutionary game theory uses the results of classical game theory and treats these preferences as differences in fitness. The paradigm game for altruism is the Prisoner's dilemma. In evolutionary game theory, the game is iterated, that is, played over and over, each play affecting the other. Results given by this iteration show that there are two "stable" strategies (in the sense given by Maynard Smith as the least "invadable" by other strategies) and they are called "Defect" and "Tit-for-tat". Roughly they go as follows: In Defect, the payoff matrix shows that it is better for player 1 to defect, no matter what player 2 does. Also, it is better for player 2 to defect no matter what player 1 does. Though it would be better for both to cooperate, neither wants to run the risk of being a "sucker" when the other player decides to defect. In Tit-for-tat, the strategy is to cooperate at first, and from then on do as the other player did in the last game. Yet, since both strategies are equally stable, the question becomes why cooperation should evolve as a strategy at all. Maynard Smith supposed that the early stages of the evolution of a cooperative strategy would have to be something like reciprocal altruism, and claims that this is what Trivers' original hypothesis could be used for.

This move makes it more clear what the assumptions behind evolutionary game theory are. The obvious problem is exactly the same as for reciprocal altruism and kin selection theories: how does the recognition get generated? We saw above that in kin selection, it is clear that kin selection cannot work unless there is a kin recognition system. In reciprocal altruism, there must be a means by which individuals can both recognise and remember a "kind act". And again, this explanation depends upon a recognition system, or at the very least, a memory system. Game

theory approaches to symbiosis are confined to species that can recognise other individuals and remember how they act.

Altruism in the sense of kin selection can take place only on an intraspecies level, and for this reason I would suggest that it is a rather uninteresting version of symbiosis. Game theory also attempts to explain cooperative behaviours that occur between animals that have memories. Earlier it was noted that using the term symbiosis to describe such relationships gives symbiosis a rather too broad characterisation. Any relationship at all might be called symbiotic if it is merely used to denote cooperative behaviours in a species. As Margulis recommends, the more interesting definition of symbiosis is to be found at the intersection of widely divergent species, where there is no possibility of genetic relatedness. The whole 'altruism' area of debate has been recognisably subverted by the neo-Darwinist population genetics approach, in the sense that cooperation and anything else evolutionary is seen to be explainable only through an analysis of gene frequency in a population. These approaches really do not describe symbiosis, but rather, the cooperative behaviours that exist in complex animal societies. Yet these type of approaches have been 'pushed' to extremes to try to account for symbiosis among non-genetically related species, as we shall see.

Axelrod and Hamilton attempted to show that the evolutionary game theory results were not confined to complex animal societies.¹⁶ Axelrod and Hamilton explicitly claim that their approach deals with "symbiosis" (pages 90, 91, 101, 219*n*). They sought to explain how a simple life form like a bacterium could form a cooperative relationship if it was limited to continuous contact with only one other organism. This would eliminate the need for a recognition system.

When an organism is not able to recognise the individual with which it had prior interaction, a substitute mechanism is to make sure that all of its interactions are with the same player. This can be done by maintaining continuous contact with the other. This method is applied in most mutualisms, situations of close association of mutual benefit between members of different species.... Another mechanism for avoiding the need for recognition is to guarantee the uniqueness of the pairing of individuals by employing a fixed place of meeting.¹⁷

¹⁶ Axelrod, R. *The Evolution of Cooperation* (Basic Books, New York 1984)

¹⁷ Axelrod p.100

Thus the explanation of how associations between different species can be cooperative in the absence of a recognition system seems to appeal to the fact that such associations have certain characteristics: continuous association with one partner, a fixed spatial meeting place. But surely the evolution of these characteristics is what needs to be explained by evolutionary game theory. Noting that such situations are stable does little to explain how they can come about. Certainly it is the case that symbiotic partners do in fact have continuous association in a fixed spatial area, but surely why this association begins is that which must be explained.¹⁸ The ‘early stages’ in the evolution of such stable associations are not addressed by the evolutionary game theory approach. Given that the competitive strategy is as stable as the cooperative strategy no matter what the probability of continuous interaction in future, the problem of how cooperative behaviour evolved is still an issue. And again, evolutionary game theory appeals to another associated type of cooperation, kin selection, to explain the early stages.

In fact ALL D [“Defect”] is evolutionarily stable no matter what the probability is of interaction continuing. This raises the problem of how an evolutionary trend to cooperative behaviours could ever have started in the first place [...] Genetic kinship theory suggests a plausible escape from the equilibrium of ALL D [...].¹⁹

But kin selection theory *itself* depends on a kin recognition system of some kind, precisely what Axelrod and Hamilton were concerned to avoid the necessity of. In addition, remember that Axelrod and Hamilton are trying to explain how non-genetically related organisms could cooperate given that they have no complex intelligence. Kin selection could never work as an early stage in the evolution of such a system, since the parties involved are not genetically related. This is the whole point of symbiosis, that the partners are completely different from one another in the sense that they have different requirements for survival, and yet are involved in a close association. For members of the same species, cooperation may appear to

¹⁸ And quite why such a spatio-temporally restricted situation would have any bearing on the need for recognition at all is interesting, perhaps it is a case of familiarity *not* breeding contempt. Also, there is no such thing as a single bacterium.

¹⁹ Axelrod p.96

be cooperation in the interest of some shared goal²⁰ for both parties, but in symbiotic associations between vastly different organisms, these goals may well be different for each partner.

It seems that all three of these approaches, kin selection, reciprocal altruism and evolutionary game theory, depend on each other for support, since they all presuppose each other. Maynard Smith appeals to reciprocal altruism for support to explain how cooperation could evolve in the early stages. Axelrod and Hamilton appeal to kin selection to the same ends. Kin selection appeals to reciprocal altruism to explain how non-genetically related partners might come to behave in altruistic associations. All of them seem to presuppose a complex social intelligence, since all need a recognition system to work. They are thus confined to intra-species cooperation among highly socially competent species. When trying to explain cooperative behaviours among distantly related species, they all seem to end up appealing to intra-species explanations for the early stage of the evolution of such associations.

Conclusion

There are two points worth drawing out of the above analysis. First, both the altruism and game-theoretical approaches are based on the assumption that nature is competitive, and cooperation is a strange case that needs to be explained. The presence of this basic assumption causes these approaches to be based largely on inter-species considerations, resulting in the claim that cooperation is explainable by the attempt to ensure that one's genes survive into the next generation. All interesting things are seen as occurring between members of a species, not between widely divergent species which have no obvious competitive interest in each other. Axelrod and Hamilton are forced into their absurd hypothesis (that bacteria can side-step a kin recognition system by being in contact with only one other organism) by the notion that cooperation can only occur when organism can remember a kind act and thus repay it, or remember a defection and retaliate. Second, the cost-benefit analysis approach that Margulis complained of earlier is obvious. This is also a product of the assumption that nature is essentially competitive. Above I have shown any approaches which assume competitiveness are forced to deal only with genetically

²⁰ Though I use this term without any teleological intent; I wish only to show that cooperation has some functional aspect.

related individuals, and can say nothing about symbiotic associations between different species. Also, such approaches also take the individual as the target of selection, even if the individual is considered as its genome. Yet we have already seen that in both bacteria-virus relationships and serial endosymbiosis theory the delineation of the individual is not at all straightforward.

Thus it is clear that symbiosis challenges some of the major core assumptions of neo-Darwinism. The interactions of natural selection, variation, and heredity are believed to entail that organisms adapt through the gradual accumulation of random variations, that organisms are in some sense separable from their environment, that an organism's genome is a functional unity, and that nature is characterised by competition between organisms. Symbiosis conflicts with all these assumptions, and thus symbiosis is inconsistent with neo-Darwinism. A symbiosis-based approach to evolution would therefore present a real challenge to current evolutionary theory.

I would like now to present a sketch of what a symbiosis-based approach of evolution might entail. First, symbiotic associations should be seen as sources of evolutionary novelty in their own right, rather than depending on the gradual accumulation of adaptations as a source of variation. When two or more organisms are seen as a symbiotic unit, it is possible to treat the whole as being more than the sum of its parts. I suggest that it may be better to treat symbiotic wholes not as decomposable entities, (and as I hope to have shown, this is not feasible in many cases), but rather as types of functional biological entities with differing characteristics than the traditional individual organisms than biology usually concerns itself with. For instance, as we have seen, there is a tendency to see symbiotic associations as the end result of a previously parasitic relationship. Perhaps it would be better to see them not so much in terms of what each partner is getting out of the relationship, but in terms of how the structure as a whole is functioning.

Second, I would like to propose that symbiotic systems need not be interpreted as a result of either competition or cooperation. In fact, such an either/or perspective is entirely unhelpful when discussing symbiosis, as I hope this paper has suggested. Both perspectives still force a judgement about the status of the units that make up the symbiotic whole, and thus the symbiosis cannot be treated as anything other than as a result of the interaction of its partners. Yet if we view symbiosis as participating in a higher level of organisation than its constituent members, we may be able

to gain more insights into evolution at large. For instance, many kinds of bacteria can be found in a symbiotic relationship with plants; they are involved in the uptake of nutrients from the soil into the roots of such plants. These partners are from vastly different taxonomic families, they have little in common evolutionarily in the sense that they have been subject to entirely different environmental pressures. Yet as a symbiotic association, they have in some sense been part of the same organisational system which has itself been subject to natural selection, e.g. food production and exchange of nutrients. Though separately they have no similarity in terms of evolutionary taxonomic complexity, on a higher level of organisation they are inextricably bound together. Perhaps it would be possible to taxonomise not the individual organisms themselves, but these higher organisational levels in some way. In much the same way that ecologists taxonomise various members of a food chain, as predators of various orders, one could categorise the types of activity that symbiotic associations engage in.

Finally, I would suggest that such a taxonomy could give more insight into evolving systems in a way that simply looking at the relative frequency of fitness traits in terms of organisms and their environments cannot. If an evolutionary system tends towards symbiotic relationships of certain kinds, one may gain insight into the salient factors of that evolving system in terms of stable strategic associations. This analysis would make available more information regarding the types of evolutionary relationships that are stable in the long term, and such information would be unavailable in any analysis which tries to decompose the units of the higher level organisational symbiotic whole.