The Units of Evolutionary Transition

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Maynard Smith's analysis of units of evolution is compared to traditional approaches generalizing Darwin's principles. Maynard Smith's key principle of multiplication is elaborated into a general account of the process of reproduction that integrates concepts of heredity and development and is applicable to all levels of the biological hierarchy. The amended analysis suggests a new unit of evolution, the "reproducer," which generalizes the concept of a replicator. The theory of evolutionary transition, the evolutionary origin of new levels of biological organization, is revised to reflect these amendments to the analysis of units. A three-stage scenario for evolutionary transition is suggested.

> "... any attempt to formalize an evolutionary problem mathematically obliges one to make, explicitly or implicitly, assumptions about what are the units of selection ..." (Maynard Smith, 1983, 315).

1. Introduction

John Maynard Smith developed an account of Darwinian units of evolution in the 1980s which looks superficially like others, particularly Lewontin's 1970 account of "Darwin's Principles." Where Lewontin offers principles of variation, fitness differences, and heritability, Maynard Smith offers principles of variation, multiplication, and heredity. After considering Maynard Smith's and several other perspectives on units of selection in the literature, I argue that there is a fundamental difference of theoretical perspective implicit in Maynard Smith's approach. Lewontin's principles describe capacities of things at pre-existing levels of spatial organization. The functionalist approach stemming from Williams, Dawkins and Hull depends on evolved functions of replication and interaction. Maynard Smith's principle of multiplication describes a *process* that carries capacities and functions. This difference, and the need for a process perspective on

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units, has become clear in the context of the problem of evolutionary transition: the evolutionary origin of new levels of biological organization. I amend Maynard Smith's analysis to bring it in line with my view that units of heredity and units of development are intimately linked in units of reproduction. I argue that "reproducers" are the units of evolutionary transition and describe the heuristic value of this view in a scenario for a stage model of the transition process.

2. Maynard Smith on units of evolution

I first heard John Maynard Smith's analysis of the units of evolution at a conference on optimality models of evolution at Stanford (Dupré, 1987). Maynard Smith characterized Darwin's explanation of why organisms come to be adapted in terms of what he took Darwin's definition of units of evolution to be:

> "... if there is a population of entities with multiplication, variation, and heredity, and if some of the variations alter the probability of multiplying, then the population will evolve. Further, it will evolve so that the

entities come to have adaptations ...” (Maynard Smith, 1987, 120).

A plausible interpretation of this analysis is as follows: Three properties, “M”, “V” and “H” are necessary for units of evolution. A fourth property of entities having the first three, “F” (fitness differences), is sufficient for the evolution of adaptations, provided the force of selection is not of equal magnitude and opposite sign to the force of inheritance (Brandon pers. comm.). Maynard Smith described fitness differences in the passage above as “variations altering the probability of multiplying.” Putting the point in terms of Maynard Smith’s later characterizations, units of evolution that *also* have F are units of selection. Thus, some units of evolution are also units of selection. Other units of evolution may evolve by means other than natural selection, e.g. drift. Units of selection that evolve under the constraint of Malthus’ principle, as Darwin conceived it, tend to become adapted (Darwin, 1859).

The addition of F to M, V and H in Maynard Smith’s analysis describes units of selection that must, it appears, be units of evolution. However, this conclusion does not follow. M, V, H and F are sufficient for units of selection but not all are necessary. Evolutionary geneticists routinely distinguish between selection within generations and evolutionary response to selection among generations, assigning quantities in models to represent the capacity for each in a population. Evolutionary response to selection of a trait (or of fitness itself), R, is a function of heritability, h^2, and selection differential, s. The selection differential can be expressed as a trait-fitness covariance, $\text{cov}(z, w)$ or as the variance in fitness, V_F (Falconer, 1960; Price, 1970; Lande and Arnold, 1983; Arnold and Wade, 1984; Wade and Kalisz, 1990). Thus, $R = h^2 V_F$. Taking Maynard Smith’s V and F to be described by V_F, the “opportunity for selection” (Wade, 1979; Wade and Kalisz, 1990), and H to be described by h^2, the heritability of fitness, units of selection need not be units of evolution. A population of entities with V and F, but lacking H, can be units of selection for which there is no evolutionary response. There is an “opportunity for selection” measured by V_F, but not a capacity for a response to selection, measured by $h^2 = 0$. (Any population for which there is *variance* in F entails that at least some members have non-zero probability of multiplication, hence, on Maynard Smith’s view of F, a population with V and F must also have M.) To

evolve *adaptations*, however, Maynard Smith’s analysis requires units of selection that are indeed units of evolution.

In the 1987 paper, Maynard Smith argued that evolution at the group level could not result in group adaptation unless groups multiply and have heritability. He denied that this occurs in “trait group” models where groups form by association and then dissolve into a random mating pool after group selection. D. S. Wilson (1975, 1980), the inventor of the trait group approach, has argued that this conclusion is incorrect because trait groups can have heritability even if they do not themselves multiply (Wilson and Sober, 1994; Wilson and Dugatkin, 1997; Sober and Wilson, 1994, 1998). I think Maynard Smith is right to include multiplication among the properties of units of evolution, but wrong to interpret fitness differences in terms of altering the probability of multiplying. Viability *selection* can occur in a population of entities, none of which multiply, even if they have non-zero probabilities of multiplying. For there to be an adaptive evolutionary response to trait group selection, however, *something* must multiply.

Further, I suggest that what distinguishes the Darwinian process of natural selection from mere sorting (Vrba and Gould, 1986), is that the former always involves entities that are, or are composed of, or are parts of, entities with the capacity to multiply. Trait group *selection* requires organism level multiplication, so for groups to be units of selection, organisms must be units of evolution in Maynard Smith’s sense. Following Williams, Maynard Smith argues that if organisms are the entities that multiply, then adaptations that result from trait group selection are not group adaptation. Wilson argues that group adaptation can result from organism multiplication with differential effects on group traits because heritability at the group level does not require group level multiplication. Group heritability is carried by the processes of organism multiplication, group formation and dissolution. Thus, whether one endorses the monistic, parsimony perspective that group adaptation explanations are to be avoided or the pluralistic, multilevel selection perspective that adaptation explanations apply at every level where there is evidence for quantitative models expressing the Darwinian properties, it is critical to understand the concept of multiplication central to Maynard Smith’s analysis of units of evolution.

The relationship between units of selection and units of evolution is complex, since only sometimes are units of evolution also units of selection and only sometimes are units of selection also units of evolution. Since my purpose here is to elaborate on Maynard Smith's concept of multiplication, I will not further address the controversies over multilevel *selection*, except to speculate that relevant differences between trait or "interaction" group models and propagule pool or "breeding group" models of multilevel selection might be articulated in terms of the analysis of reproduction developed below (Wade 1996; Wilson and Dugatkin, 1997; Sober and Wilson, 1998).

Maynard Smith characterized each of the basic properties of units of *evolution* this way: "multiplication (one entity can give rise to two), heredity (entities of kind A usually give rise to A, of kind B to B, and so on), and variation (heredity is not exact) (Maynard Smith, 1983, 315). Maynard Smith tinkered with this formulation throughout the 1990s (Maynard Smith, 1991; Szathmáry and Maynard Smith, 1993; Maynard Smith and Szathmáry, 1995; Szathmáry and Maynard Smith, 1997). In these later statements, however, the problem context had shifted from adaptation and the critique of group selection to evolutionary transition. Adaptation is a process that occurs *at* levels of biological organization (Darwin, 1859; Lewontin, 1978; Sober, 1984; Lloyd, 1988; Brandon, 1990; Burian, 1992). Evolutionary transition is the process that creates *new* levels of biological organization (Buss, 1987; Maynard Smith, 1988; Maynard Smith and Szathmáry, 1995).

In this essay, Maynard Smith's concept of multiplication will be clarified in order to address the problem of evolutionary transition. I argue that Maynard Smith's multiplication principle is too vague to serve the purposes of a general account of units of evolutionary transition. An analysis of *reproduction* is offered as a refinement of Maynard Smith's concept (see also Griesemer, 2000, in press). The heuristic value of this proposal lies in the finer grain of description afforded for processes of evolutionary transition when units are interpreted as "reproducers," entities with some of the properties of both "replicators" and "vehicles/interactors" as characterized by Dawkins and by Hull (see below). In particular, the role of development in heredity and reproduction is conceptualized more broadly, and with less dependence on a single level of organiza-tion, than growth and differentiation of multicellular organisms. Thus, the reproducer approach extends the concept of development to the multilevel framework, as selection and (to a lesser degree) heredity have been extended previously by multilevel theorists (e.g. Price, 1970, 1972; Wade and McCauley, 1980; Slatkin, 1981; Arnold and Fristrup, 1982; Heisler and Damuth, 1987; Wade, 1996; Frank, 1998; Sober and Wilson, 1998). Together, this triumvirate of extended concepts can be used to develop a general framework for the *multilevel* problem of units of evolutionary transition.

3. Multiple perspectives on the units of evolution

In 1987, I interpreted Maynard Smith's analysis as a slight variation on Lewontin's generalization of "Darwin's Principles" (Lewontin, 1970). Thus, it appeared that there were two main traditions of thought about units of selection, one deriving from Lewontin, and the other stemming from Williams' critique of group selection, extended by Dawkins and modified by Hull (Williams, 1966; Dawkins, 1976, 1983; Hull, 1980, 1981, 1988). I now think that Maynard Smith's analysis contains an essential insight lacking in other definitions of units of evolution and/or selection and that his perspective on the process of multiplication provides a helpful supplement to multilevel pluralism of perspectives on units of evolution. (In defense of pluralism, see Sober and Wilson, 1998.)

In this section, I describe Maynard Smith's perspective in light of the main traditions. The key point can be traced from Darwin's introduction of the principle of natural selection:

> "Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. ... I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection ..." (Darwin, 1859, 61).

Lewontin generalized Darwin's principles by abstracting its terms – particularly the term 'individual' – from Darwin's implicit reference to organisms and the organism level of spatial organization:

1. Different individuals in a population have different morphologies, physiologies, and behaviors (phenotypic variation).

2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness).

3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable).

These three principles embody the principle of evolution by natural selection. While they hold, a population will undergo evolutionary change (Lewontin, 1970, p. 1).

Lewontin treated references to individuals as applying abstractly to individuals of a population at any level of the biological hierarchy for which the relevant "principles" hold. These principles mention quantities that describe quantitative roles of causal capacities (Woodward, 1993) – the opportunity for selection and heritability, as discussed in the previous section. Lewontin illustrated the utility of this abstract Darwinism by applying his generalization to selection phenomena at a variety of levels of organization (Lewontin, 1970).

Lewontin's analysis was the starting point for many efforts to resolve philosophical and scientific controversy over the units of selection (e.g. Hull, 1980, 1981, 1988; Wimsatt, 1980, 1981; Lloyd, 1988; Brandon, 1982, 1990; Sober, 1984; Sober and Wilson, 1994). The "additivity criterion" for context-independence of variance components generalized Lewontin's heritability condition for units of selection (Wimsatt, 1980, 1981). Lloyd (1988) formalized the additivity approach for all levels of a compositional hierarchy, building also on Hull's replicator/interactor distinction (Hull, 1988).

In the additivity approach, the entities of one level are component parts of entities at the next level up. To be units of selection, entities at a level must have an additive, context-independent component of variance in fitness that does not appear as an additive component at any lower level (Wimsatt, 1980; Lloyd, 1988). The significant units of selection above the level of the gene, on this view, are Hull's interactors rather than Dawkins' replicators. Interactors are entities that interact directly with their external environment in such a way that replication is differential, while replicators are entities that pass on their structure directly, or largely intact, in replication (Hull, 1988, see below). The additivity con-

cept of units of selection formalized and extended Lewontin's criteria for judging when to count the properties at the higher level as the result of and subject to higher level forces and when to count them as effects of lower level forces. Subsequent discussions turned on the issue of distinguishing the operation of evolution by natural selection *at* the higher level from lower level evolution resulting from selection at the higher level ("group selection II" vs. "group selection I," Heisler and Damuth, 1987; Damuth and Heisler, 1988; cf. Sober and Wilson, 1998).

Lewontin's hierarchical approach to units of selection articulated the possibility of selection operating at many levels simultaneously. It took for granted, however, the *existence* of a hierarchy of entities that are *potential* candidates for units of selection. Darwin's concept of inheritance in the quoted passage has two senses: heritability (a capacity) and inheritance (a process that carries the capacity). Lewontin abstracted the first, taking the second as a given for entities in the familiar biological hierarchy. Maynard Smith's concept of multiplication emphasizes the second sense. His concept of heredity covers both senses. Maynard Smith's approach makes units of evolution (satisfying M, V, and H) more basic than units which may evolve *by means of* natural selection (also satisfying F). By making F secondary to the other properties in his units analysis, Maynard Smith draws attention to the evolutionary problem of the origin of levels of the hierarchy itself: under what conditions will entities evolve that are capable of being units of evolution and/or selection at that level? Selection can occur at a level only if there are entities at that level which are *capable* of being units of selection, i.e. the kinds of things that can have variance in fitness. It is the project of a theory of evolutionary transition to explain the evolutionary origin of entities with such capacities. This is a different and conceptually prior problem to that of theoretical description or empirical measurement of conditions for the *operation* of selection at a level.

A different perspective on multilevel evolution than the additivity/capacity approach stems from Williams' concept of an evolutionary gene. Williams wrote: "… I use the term *gene* to mean 'that which segregates and recombines with appreciable frequency'" (Williams, 1966, 24). That is, the gene is a kind of entity which is stable to processes that tend to disrupt structure across generations. Organ-

isms are less stable in this sense than genes, but due to the fairly direct relationship between genotype and phenotype, organisms can become adapted through the process of evolution by natural selection. Because groups are much more ephemeral than organisms, parsimony dictates that adaptation not be attributed directly to them if explanations in terms of lower levels are available. Whether this perspective is a rival or a complement to the additivity view has been the subject of intense debate ever since, although the tide may be turning toward the latter (Sober and Wilson, 1998).

Dawkins pushed Williams' argument to its logical conclusion in his concept of a "replicator": even organisms do not have the kind of stability necessary to be the bearers of evolutionary adaptation. They, like groups, and in general, like all "vehicles" of the units of selection, are destroyed each generation. Only replicators have sufficient stability, longevity, and fecundity (1976) to be units of selection. In the sequel to *The Selfish Gene*, Dawkins articulated his view of replicators:

> "I define a *replicator* as anything in the universe of which copies are made." … "An *active replicator* is any replicator whose nature has some influence over its probability of being copied." … "A *germ-line replicator* (which may be active or passive) is a replicator that is potentially the ancestor of an indefinitely long line of descendant replicators." … "The reason active germ-line replicators are important units is that, wherever in the universe they may be found, they are likely to become the basis for natural selection and hence evolution." … "The world tends automatically to become populated by germ-line replicators whose active phenotypic effects are such as to ensure their successful replication." (Dawkins, 1983, 83–84.)

Hull modified Dawkins' analysis, distinguishing two senses of "interaction" that Dawkins had confounded (Hull, 1980, 1981, 1988). Dawkins' replicators and vehicles are best understood, Hull argued, in terms of the relative directness of two kinds of interaction: selective interaction with the external environment and interaction to pass on structure in replication (Hull, 1988). Replicators do the former sort of interacting indirectly and the latter directly, while vehicles, which Hull calls "interactors," reverse these degrees of directness. Hull defines replicators and interactors as follows:

> *replicator* – an entity that passes on its structure largely intact in successive replications.

> *interactor* – an entity that interacts as a cohesive whole with its environment in such a way that this interaction *causes* replication to be differential (Hull, 1988, 408).

Although there are points in common between Dawkins' and Hull's analyses of units, they come to strongly different conclusions about what are the significant units in evolution: Dawkins argues that genes, because they are replicators, are the important units of selection, while Hull argues that entities across the biological hierarchy are important units of selection when they function as interactors. Both agree that entities above the level of genes are unlikely to function as replicators and that the hierarchy of vehicles or interactors has evolved to separate the replicator and interactor functions in a more efficient division of labor than at the origin of life when replication and interaction functions may have been fulfilled by the same entities, perhaps RNA molecules.

Maynard Smith and Szathmáry (1995, p. 8) endorsed the "gene's eye view" of Williams and Dawkins for the purposes of developing evolutionary transition theory. I do not think a choice was necessary because the perspectives should not be seen as rivals, but rather as complementing components of a robust theory. The Williams–Dawkins–Hull approach to units complements the Lewontin–Wimsatt–Lloyd approach in offering a functional description of entities at any spatial level of organization that can have the properties required by the additivity analysis. Entities that have heritable variance in fitness are entities that are (or are composed of) replicators or interactors in Hull's sense. Whether they do in fact have the relevant properties is an empirical question, not a theoretical one. Whether entities at a given level are *likely* to function as replicators or interactors (or both or neither) is also empirical. By focusing on function, Dawkins and Hull avoid the *assumption* of hierarchy built into the Lewontin approach. However, their analyses of replicators and interactors implicitly appeal to highly evolved properties of DNA (passing on structure intact in "replication") and organisms ("interacting with an environment" so that replication is differential). Because these properties are themselves products of evolutionary transition, the replicator and interactor functions still do not fully resolve the units problem for evolutionary transition theory.

In my view, Maynard Smith's approach to units of evolution offers a much needed third perspective. The familiar approaches to units of evolution take for granted either the hierarchy of entities which are at least potentially capable of evolving or the functional properties that allow evolution to occur. Maynard Smith's foundation in the process of multiplication rather than selection or variation frees units analysis from dependency on concepts of selection and evolution. The value added by Maynard Smith's analysis lies with a different problem than group or multilevel selection. This only became clear in light of the new work it was made to do for the problem of evolutionary transition (Maynard Smith and Szathmáry, 1995).

In the same year that Maynard Smith applied his analysis of units of evolution to optimality models of adaptation, Leo Buss published an important book on the problem of evolutionary transition (Buss, 1987). When Maynard Smith explored the logic of this problem in the wake of Buss's and others' arguments (e.g. Margulis, 1981), different elements of his units analysis came to the fore than Lewontin's emphasis on fitness variance and the units of selection (Maynard Smith, 1988). In particular, the fundamental nature of heredity became a central conceptual concern rather than the representation in response to selection models and measurement of its quantitative role as heritability.

The inexactness of heredity became prominent in the analysis of the evolutionary transition from chemical to biological systems (Maynard Smith, 1983; Maynard Smith and Szathmáry, 1995; Szathmáry and Maynard Smith, 1993, 1997; Szathmáry 1999a, 1999b). In autocatalytic chemical systems molecules catalyze exact copies of themselves. In genuine biological systems of heredity, mutant molecules make more mutants. The heritability of traits depends on the fundamental capacity of variant trait determinants to catalyze variant determinants. Merely autocatalytic systems are not units of evolution. The key to the earliest evolutionary transition – the origin of life – is to understand how molecular systems with both heredity and variation could arise from autocatalytic systems. This problem is easily formulated from Maynard Smith's perspective on units of evolution. While not incompatible with the other perspectives, their attention to selection does little to promote exploration of this aspect of heredity.

In the next section, I focus on Maynard Smith's multiplication principle and argue that it is the key to integrating units of development and heredity. In subsequent sections, I offer an analysis of reproduction based on the integration of heredity and development that refines the multiplication principle as the basis of units of evolutionary transition.

4. Biological multiplication entails development

The problem of evolutionary transition is to explain the evolutionary origin of new levels of spatial organization and to characterize how the generalized functions (replication, interaction) and capacities (opportunity for selection, heritability) described by Darwin's principles are implemented at those levels. The process perspective can aid understanding of this problem. Maynard Smith's principle of multiplication describes a process which need not in turn be explicated in terms of evolutionary concepts, even if all modern biological multipliers are products of evolution. Evolution involves the interaction of multiplication with other processes such as natural selection. Multiplication is fundamental to all evolutionary processes because units of selection either are units of multiplication or are composed of units of multiplication. However, Maynard Smith's description of multiplication is incomplete. Filling in the details will lead to the account of biological reproduction offered in the next section.

Maynard Smith's variation principle is dependent upon the heredity principle because, as noted above, V states that H is "inexact." In early statements of his view, Maynard Smith characterized M as independent of H. In Maynard Smith (1983), multiplication meant that one entity can give rise to two. (The word 'can' suggests that Maynard Smith had a capacity rather than the process that carries the capacity in mind, as in Lewontin's strategy. Later statements of the principle drop the 'can'.)

In later statements, M and H interlock. The entities multiplied are not merely distinct objects, they are *alike in kind*. Heredity is the principle that "like begets like." Szathmáry and Maynard Smith (1993, 198) define the component principles this way:

> (1) Multiplication: If there is entity A, then it must give rise to more *of the same*. (emphasis added)

(2) Heredity. Like begets like: A type entities produce A type entities, B type entities produce B type entities, and so on.

(3) Variability. Heredity is not exact; occasionally A type objects give rise to A' type objects (it may be that A' = B).

If objects of different types have a hereditary difference in their fecundity and/or survival, the population undergoes evolution by natural selection.

A still later statement of *M* is even more explicit:

Multiplication. Entities should give rise to more entities *of the same kind*. (Szathmáry and Maynard Smith, 1997, emphasis added)

The precise nature of this condition on multiplication is vague. Any two things are similar in an indefinite number of ways, so every two objects produced by multiplication are of the same kind. The question is, what are the *relevant* kinds for a theory of evolutionary transition? Concepts of variation, fitness and heritability have been generalized in units analyses of Darwin's principles. I suggest that the concept of development, the process through which sameness of kind is achieved, has not been similarly generalized and incorporated into units analyses. Some authors have noted that evolution is a three step process rather than two steps (variation production and selection, Mayr, 1988, p. 97) because it involves component processes of selection, reproduction *and development* (Brandon, 1990, p. 5; Burian, 1992). If development is understood in terms of the traditional, idealized mapping of genotype to phenotype, however, there is a problem for analyzing units of evolutionary transition. The genotype-phenotype map is *itself* a product of evolutionary transition and thus should not be made axiomatic in the definition of units of evolutionary transition for the same reason that levels of organization cannot be assumed.

The problem of making the concept of multiplication precise and relevant to units of evolutionary transition, therefore, is one of specifying the relation between heredity and development. Just as our conceptions of heredity have been shaped by modern genetics, which makes genes the sole or primary explanatory units of heredity, conceptions of development are shaped by our modern understanding of multicellular growth and differentiation. But these are manifestations of particular levels of organization, just as our theories of the genotype-phenotype map are based on pretransition thinking, so we must step back from conventional understanding and look deeper into the problem.

For purposes of evolutionary theory, the process of development can be understood most generally as the acquisition by offspring of the same relevant kind as the parent(s) (Griesemer, 2000, in press). Our common notion of this kind is the set of species typical traits that parents and offspring reliably share. Giraffes make more giraffes and *E. coli* make more *E. coli*. It is notorious, however, that species do not have "essences." They are, instead, historical individuals (Hull, 1988; Ghiselin, 1997). Even if we put that philosophical issue aside, it is problematic to rely on species typical traits as a way of interpreting development. Alternation of generations (e.g. between winged and non-winged insect forms), metamorphosis within generations, phenotypic plasticity, and modularity allow parts and individuals to have substantially or even radically different structures, suggesting that no particular morphology must be typical of the parts or organisms of a given species.

What is common to these and other challenging cases such as chimaeras, symbioses, and mutualisms is that traits acquired in development can be interpreted in terms of their evolutionary consequences. This is the key insight of the functionalist school of thought on units (shared by the multilevel approach of Sober and Wilson, 1998). Let evolution pick out the relevant properties of units. A trait that functions in an interactor in a given population and environment to alter the probability of that interactor's expected reproductive success contributes to the interactor's acquisition of the capacity to reproduce. The limitation of the functionalist approach is that it derives insight about general functions without regard to the transition problem of origination of these properties. Hence it neglects the need for a developmental perspective on units of heredity.

Development from an evolutionary point of view can be thought of, in general, as the acquisition of the capacity to reproduce. Acquisition of a particular trait that plays a causal role in a mechanism of development can be analyzed in terms of this general, developmentally acquired capacity to reproduce regardless of the specific ways or degrees in which traits contribute to it.

Thus, Maynard Smith and Szathmáry's addendum to the principle of multiplication – sameness of kind – can be understood as the result of exercising a general developmental capacity to acquire the capacity to reproduce. The common sense concept of

development as the acquisition of species typical traits is, from an evolutionary point of view, a *maximal* concept because greater similarity would entail that new species could not evolve. This evolutionary bound on the principle of multiplication complements the bound asserted in Maynard Smith's principle of variation. If heredity were exact, then evolution would come to a halt when the standing variation that primed the evolutionary process had been used up. If the "same kind" yielded by development were any more exacting than species typicality, heredity would be too limiting for the evolution of new species.

Development interpreted as the acquisition of the capacity to reproduce is an evolutionary *minimum* concept of development. Whatever else development is, it must meet this minimum or else multigenerational evolutionary processes would be impossible. Most of the interesting theoretical and empirical problems of evolution and development lie between these maximum and minimum bounds. Wherever the interesting problems lie, the multiplication principle entails development and development is directly related to the analysis of heredity through the connection of both to reproduction.

5. Reproducers

Let us examine the main part of the concept of multiplication, now that the addendum has been made more precise. Multiplication is the process by which more entities are produced. This too is vague. First, biological multiplication is of *material* objects. Second, the relation between parents and offspring is not merely one of resemblance, but rather is one of *material overlap*. Offspring are made from parts of the parents, they are not merely similar objects made from wholly distinct materials. Otherwise, copying would be the appropriate concept for biology rather than multiplication. Copying, however, fails as an appropriate analysis of biological multiplication (Griesemer, in press).

The reason biological multiplication involves material overlap of parents and offspring is due to the demands of development. Development is minimally the acquisition of the capacity to reproduce. For multiplication to result in more entities *of the same relevant kind*, the offspring must be *organized* so as to have – autonomously from their parents –

the capacity to develop. That is, offspring must be born with the capacity to acquire the capacity to reproduce. While it is conceivable that this degree of organization could be transmitted to unorganized bulk matter, it is not probable that a system of multiplication with this kind of spontaneous, induced, developmental organization could compete with any known biological systems in which highly organized material propagules form the basis for the origin of new entities. Even Dawkins, who generally attributes all significant biological causal powers to replicators because he accepts the Weismannist causal logic for biology (Dawkins, 1983, 164), admits that development must play this "bootstrap" role in order for replicators to function (Dawkins, 1995). The issue raised here is not the empirical one of whether development in life cycles is favored by selection because it leads to complex adaptations (Dawkins, 1983, ch. 14). It is rather that the concept of multiplication entails a concept of development.

The process of reproduction can be analyzed as multiplication of material overlapping propagules that confer the capacity to develop, specified in terms of the minimum notion of development as acquisition of the capacity to reproduce (Griesemer, 2000, in press). The interlocking of developmental and reproductive capacities is recursive. The realization of a reproduction process entails the realization of a developmental process. The realization of development entails reproduction. The recursion "bottoms out" in a condition of "null development."

An example of reproduction with null development is chemical autocatalysis. Autocatalytic molecules just *have* the capacity of autocatalysis; they need not *acquire* it through "development." Moreover, heredity is likely to be exact whenever development is null. Variation "emerges" in the developmental process of acquiring the capacity to reproduce. Null developers need not acquire reproductive capacity, so the opportunity for variation which nevertheless leads to reproductive capacity is absent. Chemical autocatalysis probably formed the basis for the origin of living systems from non-reproductive chemical systems (Gánti, 1971, 1979, 1997). Theories of the origin of life must explain the transition from exact to inexact heredity and from autocatalysis with null development to reproduction with development.

The definition of reproduction as multiplication with material overlap of propagules with develop-

mental capacity does not entail, however, that the recursion must cascade down levels of *spatial* organization. The recursion involves levels of development as well as levels of reproduction and the former may cascade *up* levels of spatial organization. One can imagine that successful reproduction of an organism, for example, may require the "development" of a social group of which the organism is a part. Chromosome reproduction may entail cell development. DNA reproduction may entail chromosome development. Indeed, the dependency of formerly independent replicators on the "replication" of the wholes – the basis for the definition of evolutionary transition (Maynard Smith and Szathmáry, 1995, 6) – is a *developmental* dependency that should be incorporated into the analysis of units (see Szathmáry and Maynard Smith, 1997).

The successful reproduction of a DNA double helix depends on the development of the cell in which it resides. The semi-conservative replication of DNA satisfies the requirement of material overlap. The molecular structure of nucleic acid polymers carry a "developmental" capacity for templating which is conferred on daughter molecules. However, the *realization* of molecular developmental capacities – the acquisition of another round of "replication" – requires acquisitions by the cell. DNA cannot "replicate" in a vacuum.

In contrast to reproduction, copying does not entail material overlap. The resemblances implied by copying processes are generally insufficient to meet the evolutionary minimum requirement, *unless* the copying occurs in the context of a more inclusive process of reproduction as outlined above. It is possible to make the "gene's eye view" work as an analysis of units of evolution (replicators) only in so far as replication (interpreted as copying) takes place in host reproducers serving as interactors. The process of replication cannot be completely analyzed without taking the context of reproduction processes into account, however, because the developmental realization of the capacity of a replicator to replicate can only be specified in the context of the reproducer.

The same point applies to memes. *Wherever* there is a Dawkins-replicator, one will find a system of biological reproduction as well. Thus, there is an alternative way to interpret what replicators *are* that is compatible with the analysis of reproduction on offer in this essay. This alternative turns out to be suggestive about the structure of evolutionary transitions.

If the acquisition of the capacity to reproduce is the evolutionary minimum concept of development, we can consider less minimal notions as well. A cleavage cell's acquiring the capacity to reproduce might mean little more than taking in the nutrients needed to synthesize DNA and activate the mitotic spindle apparatus. The spindle apparatus, however, is highly evolved. If development requires the *evolved* behavior of material propagules transmitted from the parent, rather than, for example, the mere physicochemical diffusion of substances from the environment across spontaneously formed coacervate membranes, then I will call the reproduction process an *inheritance* process and its units "inheritors." One reason to call such processes inheritance processes is that epigenetic inheritance systems as well as the nucleic acid genetic system satisfy this restricted form of reproduction (see Jablonka and Lamb, 1995).

Moreover, let us call the genetic system a system of *replicators* because the highly evolved genetic mechanisms that play a role in development have the particular character of a coding system. Put differently, replicators are evolved reproducers having the properties of "digital" or "unlimited heredity," in which the number of combinatorially possible states of the system vastly outnumbers the actual individuals in any reasonable population (Jablonka and Szathmáry, 1995; Szathmáry and Maynard Smith, 1997; Szathmáry, 1999b). This combinatorial structure is put to use evolutionarily by means of coding processes in development. A coding process is a process that generates a mapping between a code source and a code recipient, e.g. between a DNA molecule and a protein molecule. "The" genetic code is sustained by such a coding process.

Thus, rather than thinking of 'replicator' as a generalization of the gene or the genotype concept, *replicators* – units of replication – are a special class of *inheritors* – units of inheritance – which in turn are a special class of *reproducers* – the units of reproduction – which in turn are a special class of multipliers. There is a hierarchy of concepts of which 'replicator' is the most specialized (Figure 1).

The class of systems of concern to biology in general are the reproducers, not the multipliers because the latter includes copiers as well as reproducers.
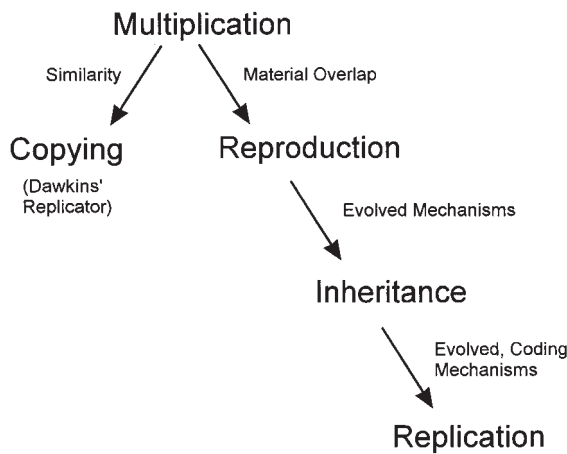
Multiplication

Similarity   Material Overlap

Copying   Reproduction
(Dawkins'
Replicator)

                                     Evolved Mechanisms

                        Inheritance

                                     Evolved, Coding
                                     Mechanisms

                        Replication

FIG. 1. Tree of multiplication concepts
The special features of each type of multiplication (see text for discussion) are indicated next to the arrows, which form a hierarchy. Each arrow points to a special case of the process higher in the hierarchy, which thus has the properties higher in the hierarchy as well. Replication is a special case of inheritance, inheritance is a special case of reproduction, and so forth. Copying is a kind of multiplication which does not distinguish material from abstract cases, e.g. memes

Moreover, because the class of reproducers includes systems with so-called "epi-genetic" inheritance as well as genetic replicators, claims about replication and epigenesis can be interpreted in the common framework of reproducers. I propose a simple modification of Maynard Smith's analysis of units of evolution: substitute reproduction as analyzed above for multiplication. Further, this modification suggests a specific amendment to the Maynard Smith and Szathmáry (1995) characterization of evolutionary transition, described in the next section.

6. The units of evolutionary transition

A common feature of the entities that go through evolutionary transitions from which emerge new levels of spatial organization and complexity is that "… entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it" (Maynard Smith and Szathmáry, 1995, 4; Szathmáry and Maynard Smith, 1995, 227). As a function of this fundamental feature, there tends to be a division of labor among component parts of an inclusive whole because of the increased efficiency that results from task specialization. A major focus of contemporary evolutionary research is to understand how a division of

labor, which may also create a conflict of replicator interests, can be enforced. Put differently, the problem is why the component entities of the larger whole, which once were independent replicators, do not subvert the cooperative order "from below" under conditions where independence may be favored. Meiotic drive and transposons subvert fair meiosis, which equalizes the interests of genes linked in (autosomal) chromosomes. Parthenogenesis subverts the equalizing effects of sexual reproduction. Cancers subvert the cooperative behavior of differentiated somatic tissues by escaping from the growth controls placed on somatic cells. Egg-laying worker bees subvert the genetic interests of non-reproductive castes of haplo-diploid social insects whose genes are unusually highly related (Maynard Smith and Szathmáry, 1995, 6–7). Why does not subversion from below defeat evolutionary transition?

Through the major transitions in the history of life, there have also been changes in the *mode* of replicator information storage and transmission, including the evolution of the genetic code, sexual reproduction, epigenetic inheritance, and human language. Major transitions include the origin of: chromosomes, eukaryotes, sex, multicellularity, and social groups (Szathmáry and Maynard Smith, 1995, 227).

Subversion of the changed modes of information storage and transmission achieved by evolutionary transitions may be prevented, and the transition maintained, by contingently irreversible events unrelated to the selection processes that led to the transition (Maynard Smith and Szathmáry, 1995, 9). The mechanisms of development that evolve in such a way that cooperating groups of replicators increase their chances of replicating may be such that escape from the collective becomes effectively impossible. Once symbiotic mitochondria lost genes to the nucleus, they no longer could survive as independent entities. Such mechanisms maintain the transition by altering the genetic interests of component entities in the direction of cooperation (Hurst et al., 1996; Haig, 1997).

The analysis of reproduction in the previous section raises questions about this account of evolutionary transition. First, if transition requires replicators which replicated independently before the transition and replicate as dependent parts of a larger whole afterwards, then we should expect to find replicators at

every transition level. This is implausible if the "gene-centred approach" endorsed by Maynard Smith and Szathmáry is correct. According to that approach, genes are the only likely biological replicators. Thus, there would likely be only one evolutionary transition – from a situation where genes replicate independently to where they replicate as dependent parts of a larger whole. Perhaps this transition occurred with the invention of hypercycles (Eigen and Schuster, 1977).

Szathmáry and Maynard Smith (1997, 568) acknowledge this problem. They make use of the concept of a reproducer which integrates units of heredity and development, in contrast to the anti-developmental concept of a replicator, to interpret higher level transitions: "(i) it is reproducers, rather than replicators, of a higher level that arose during the transitions; (ii) when a higher level reproducer appears, a novel type of development is worked out; and (iii) rather old-fashioned replicators are packaged into novel reproducers."

Viewing the relation between replication and reproduction as Szathmáry and Maynard Smith have is to adopt Dawkins' gene's eye view, in which replicators are rare and the subjects of a fundamental process (replicator selection) while interactors (reproducers) are common, hierarchically organized subjects of a derivative process (vehicle selection). I argue for a more radical perspective, in which replicators are viewed as a special class of reproducers whose development is deeply dependent on many higher levels of reproductive organization. Replicators are deeply dependent because successive evolutionary transitions have altered their mode of transmission and information storage – i.e. their mode of *development* – several times over. Far from being master molecules, genes are prisoners locked in the deepest recesses of a hierarchy of prisons. They do escape from time to time. These outbreaks, analyzed in the literature on genetic conflicts, reveal much about the developmental dependencies of genes.

But what recommends taking this more radical view of replicators? I suggest the following heuristic scenario for evolutionary transitions. Evolutionary transition theory aims to analyze trends of increasing complexity. As Bonner (1965, 1974, 1988) and Dawkins (1983) argue, adaptive complexity can only evolve if life cycles through a bottleneck that resets the developmental process. For multicellular organisms, life cycles through a single cell bottleneck (Grosberg and Strathman, 1998). In general terms, one can imagine a progression in evolutionary transitions of developmental "modes" from the general to the specific: from reproducers, to inheritors, to replicators. That is, evolutionary transitions involve one to three stages in the evolution of development at each new level of reproduction. Reproducers are entities that multiply by material overlap of propagules conferring the capacity to develop. Inheritors are entities that multiply by material overlap of propagules conferring the capacity to develop by *evolved* mechanisms. Replicators are entities that multiply by material overlap of propagules conferring the capacity to develop by evolved, *coding* mechanisms. Suppose we hypothesize that this logical progression were an actual, historical progression for at least some episodes of evolutionary transition?

Such a hypothesis, in contrast to the replicator interpretation, would suggest that evolutionary transitions are not, or need not be, *mere* "point" transitions from independent replication to dependent replication within larger wholes. Rather, they may be extended processes with several potentially identifiable stages. The first stage – the origination of a new level – would require the origination of reproducers composed of reproducers, though the composition may have no more structure than a coacervate droplet of chemical reaction networks or a breeding or interaction group of con-specific organisms in a local geographic area. We can characterize the first stage in this general way because reproducers are not set in opposition to replicators as Dawkins contrasts vehicles to replicators. Perhaps the old, independent reproducers *are* replicators, as is supposed in models of autonomous, self-catalytic RNAs cooperating in compartmented hypercycles or proto-chromosomes. But perhaps they are only inheritors or are merely reproducers, as is supposed by metabolism-first models of the origin of life (see Dyson, 1985; Morowitz, 1992). The origin of a new level of *reproduction* does not require a fancy developmental process, as would be entailed by the origination of a new level of replication. Rather, the stabilization and maintenance of a level of reproduction require a sophisticated development. Replicator-based accounts of transition seem to imply that this evolution of development must evolve coincidently with the emergence of a new level of reproduction.

In the second stage, suppose that some form of subversion from below is likely to threaten the integrity of the newly emergent, composite, cooperative reproducers. Evolution of mechanisms of development that enforce cooperation, e.g. by equalizing genetic interests, by policing rouges, or by enforcing centralized control on the means of reproduction would maintain the new level of reproducers. These are the sorts of mechanisms for stabilizing a transition that Maynard Smith and Szathmáry (1995) discuss, but their units analysis does not reflect the significance of these mechanisms as the evolution of development among newly emergent *reproducers*.

According to the reproducer analysis, the *evolution* of developmental mechanisms in stage 2 means that the now-dependent *reproducers* at the lower level, i.e. reproducer parts of the new, independent reproducers, become inheritors. The propagules of reproducers at the new level must transmit the evolved developmental capacities via the material overlap of developmental mechanisms that evolved from reproductive parts at the old level of reproduction. The demands of heredity thus place important constraints and conditions on the nature of the evolution of development at the new level. These mechanisms may behave as inheritance systems transmissible *in parallel to* the transmission system of the original reproducers or they may be propagated through transmission of capacities of lower level components (as in the discussion of trait group properties discussed above). In other words, to the extent that complex, adaptive evolution of development must occur to prevent subversion from below, the second stage of evolutionary transition will involve the evolution of a transmission system of inheritors from the developmental mechanisms that drove the first stage.

The DNA methylation systems that function as the result of gene-encoded methylation enzymes, along with the methyl patterns themselves, are systems of inheritance that satisfy the analysis of reproduction above. They multiply with material overlap of propagules conferring the capacity to develop, just as the nucleic acid genes themselves do. The "(Samuel) Butler test" for an inheritance system reveals the plausibility of this multiple-inheritance-system interpretation of genes and methylation in contrast to the usual single-inheritance-system interpretation of genes and epigenetic factors. Butler is famously said to have remarked that a hen is an egg's way of making another egg. If it makes sense to say that a gene is a methyl pattern's way of making another methyl pattern – that a gene is part of the developmental mechanism of methyl reproduction – then it makes sense to call the methylation system an inheritance system in the sense defined above (see Gray 1992 for the development of this style of argument).

A third stage of evolutionary transition would be reached when the evolved mechanisms of development become a full-fledged coding system. It is commonly believed that there are only two such coding systems: the nucleic acid system and human language. I am not sure this is correct. Glycoproteins may have enough combinatorial structure in their carbohydrate branching patterns to constitute a coding system at the cell surface (Palade, 1983; Sharon and Lis, 1993). Nevertheless, suppose the conventional belief is correct. The question of evolutionary transition, interpreted within the unifying framework of reproducers, may be framed as a question of heterochrony: why do some transitions appear to go through all three stages whereas others appear to compress or even skip stages? Why did the transition to prokaryotic cells involve all three stages, including the evolution of the nucleic acid coding system, while the transition(s) to multicellularity seem to have involved only the evolution of epigenetic inheritance systems for cell heredity? The evolution of a new level of *replicators* (stage 3) appears not to have been required for multicellularity. And why did the high level transition to human culture involve linguistic replicators while intervening transitions apparently did not?

But perhaps this question, arising from the refinement of Maynard Smith's units analysis, only indicates that the three stage characterization of evolutionary transition, and hence of the relations among reproducers, inheritors, and replicators is still too dependent on our conventional understanding of genetic systems. What we take to constitute genetic coding and the "digital" property that makes replicators a system of "unlimited" heredity may not be the best way to characterize stage 3. Or perhaps instead there are properties shared by coding systems other than the digital property emphasized by Dawkins (1995) and by Szathmáry (1999a, b).

7. Summary

I have argued that Maynard Smith's analysis of units of evolution, with the refined notion of reproduction in place of the vague notion of multiplication, is suitable to serve as an analysis of units of evolutionary transition. The analysis of reproduction offered here shows the value of an integrated account of units of heredity, development and evolution. Development has always been the weak theoretical link in evolutionary theory. The context of evolutionary transition sharpened the problem and it turned out that Maynard Smith's analysis of evolutionary units was suited to describe it. If the analysis of reproduction offered here is taken as a refinement of Maynard Smith's principle of multiplication, then the process of evolutionary transition can be reformulated simply as follows: entities that were capable of independent reproduction before the transition can reproduce only as parts of a larger whole after it. Because replicators are a special class of reproducers, the Maynard Smith and Szathmáry account is not contradicted, but rather is shown to be a special case that may not be appropriate to all the transitions they discuss. The relations among reproducers, inheritors, and replicators articulated above further suggest that transition may occur in one to several stages, which raises new questions about the character of transitions that do, or do not, pass through all of them. Although undoubtedly inadequate to all the facts, this scenario has the merit of suggesting directions for further theoretical work.

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References

ARNOLD, A. and FRISTRUP, K. (1982): The theory of evolution by natural selection: A hierarchical expansion. *Paleobiology* **8**:113–129.

ARNOLD, S. J. and WADE, M. J. (1984): On the measurement of natural and sexual selection: Theory. *Evolution* **38**:709–719.

BONNER, J. (1965): *Size and Cycle, an Essay on the Structure of Biology*. Princeton University Press, Princeton, N. J.

BONNER, J. (1974): *On Development*. Harvard University Press, Cambridge, Mass.

BONNER, J. (1988): *The Evolution of Complexity by Means of Natural Selection*. Princeton University Press, Princeton, N. J.

BRANDON, R. (1982): The levels of selection. In ASQUITH, P. and NICKLES, T. (eds): *PSA*, Vol. 1. Philosophy of Science Association, East Lansing, pp. 315–322.

BRANDON, R. (1990): *Adaptation and Environment*. Princeton University Press, Princeton, N. J.

BURIAN, R. (1992): Adaptation: Historical perspectives. In FOX KELLER, E. and LLOYD, E. (eds): *Keywords in Evolutionary Biology*. Harvard University Press, Cambridge, pp. 7–12.

BUSS, L. (1987): *The Evolution of Individuality*. Princeton University Press, Princeton, N. J.

DAMUTH, J. and HEISLER, I. L. (1988): Alternative formulations of multilevel selection. *Biology and Philosophy* **3**: 407–430.

DARWIN, C. (1859): *On the Origin of Species*. John Murray, London.

DAWKINS, R. (1976): *The Selfish Gene*. Oxford University Press, New York.

DAWKINS, R. (1983): *The Extended Phenotype*. Oxford University Press, New York.

DAWKINS, R. (1995): *River Out of Eden, A Darwinian View of Life*. BasicBooks, New York.

DUPRÉ, J. (ed.) (1987): *The Latest on the Best, Essays on Evolution and Optimality*. Cambridge, MIT Press.

DYSON, F. (1985): *Origins of Life*. Cambridge University Press, Cambridge.

EIGEN, M. and SCHUSTER, P. (1977): The hypercycle. A principle of natural self-organization Part A: Emergence of the hypercycle. *Naturwissenschaften* **64**:541–565.

FALCONER, D. S. (1960): *Introduction to Quantitative Genetics*. The Ronald Press, New York.

FRANK, S. (1998): *Foundations of Social Evolution*. Princeton University Press, Princeton, N. J.

GÁNTI, T. (1971): *The Principle of Life* (in Hungarian, [1986] tr. L. Vekerdi): OMIKK: Budapest.

GÁNTI, T. (1979): *A Theory of Biochemical Supersystems*. University Park Press, Baltimore.

GÁNTI, T. (1997): Biogenesis itself. *J. Theor. Biol.* **187**: 583–593.

GHISELIN, M. (1997): *Metaphysics and the Origin of Species*. SUNY Press, Albany.

GRAY, R. (1992): Death of the gene: Developmental systems strike back. In GRIFFITHS, P. (ed.): *Trees of Life*. Kluwer Academic Publishers, Dordrecht, pp. 165–209.

GRIESEMER, J. R. (2000): Reproduction and the reduction of genetics. In BEURTON, P., FALK, R. and RHEINBERGER, H-J. (eds): *The Concept of the Gene in Development and Evolution*. Cambridge University Press, Cambridge, pp. 240–285.

GRIESEMER, J. R. (in press): Development, culture and the units of inheritance. *Philosophy of Science* **67** (Proceedings): S348–S368.

GROSBERG, R. and STRATHMAN, R. (1998): One cell, two cell, red cell, blue cell: The persistence of a unicellular stage in multicellular life histories. *Trends in Ecology and Evolution* **13**:112–116.

HAIG, D. (1997): The social gene. In KREBS, J. and DAVIES, N. (eds): *Behavioural Ecology: An Evolutionary Approach*. 4th ed. Blackwell Science, Cambridge, Mass.

HEISLER, I. L. and DAMUTH, J. (1987): A method of analyzing selection in hierarchically structured populations. *Amer. Natur.* **130**:582–602.

HULL, D. (1980): Individuality and selection. *Annu. Rev. Ecol. Syst.* **11**:311–332.

HULL, D. (1981): The units of evolution: A metaphysical essay. In JENSEN, U. and HARRÉ, R. (eds): *The Philosophy of Evolution*. The Harvester Press, Brighton, pp. 23–44.

HULL, D. (1988): *Science as a Process*. University of Chicago Press, Chicago.

HURST, L., ATLAN, A. and BENGTSSON, B. (1996): Genetic conflicts. *Q. Rev. Biol.* **71**:317–363.

JABLONKA, E. and LAMB, M. (1995): *Epigenetic Inheritance and Evolution*. Oxford University Press, Oxford.

JABLONKA, E. and SZATHMÁRY, E. (1995): The evolution of information storage and heredity. *Trends Ecol. Evol.* **10**: 206–211.

LANDE, R. and ARNOLD, S. J. (1983): The measurement of selection on correlated characters. *Evolution* **36**:1210–1226.

LEWONTIN, R. (1970): The units of selection. *Annu. Rev. Ecol. Syst.* **1**:1–17.

LEWONTIN, R. (1978): Adaptation. *Sci. Amer.* **239**:212–230.

LLOYD, E. (1988): *The Structure and Confirmation of Evolutionary Theory*. Greenwood Press, New York.

LLOYD, E. (1999): Altruism revisited. *Q. Rev. Biol.* **74**: 447–449.

MARGULIS, L. (1981): *Symbiosis and Cell Evolution*. Freeman, San Francisco.

MAYNARD SMITH, J. (1983): Models of evolution. *Proc. R. S. Lond.* B **219**:315–325.

MAYNARD SMITH, J. (1987): How to model evolution. In DUPRÉ, J. (ed.) (1987): *The Latest on the Best, Essays on Evolution and Optimality*. MIT Press, Cambridge, pp. 119–131.

MAYNARD SMITH, J. (1988): Evolutionary progress and the levels of selection. In NITECKI, M. (ed.): *Evolutionary Progress*. University of Chicago Press, Chicago, pp. 219–230.

MAYNARD SMITH, J. (1991): A Darwinian view of symbiosis. In MARGULIS, L. and FESTER, R. (eds): *Symbiosis as a Source of Evolutionary Innovation*. MIT Press, Cambridge, pp. 26–37.

MAYNARD SMITH, J. and SZATHMÁRY, E. (1995): *The Major Transitions in Evolution*. W. H. Freeman, Oxford.

MAYR, E. (1988): An analysis of the concept of natural selection. In *Towards a New Philosophy of Biology*. Harvard University Press, Cambridge, pp. 95–115.

MOROWITZ, H. (1992): *Beginnings of Cellular Life*. Yale University Press, New Haven.

PALADE, G. (1983): Membrane biogenesis: An overview. *Methods Enzymol.* **96**:xxix–lv.

PRICE, G. (1970): Selection and covariance. *Nature* **227**: 520–521.

PRICE, G. (1972): Extension of covariance selection mathematics. *Annals of Human Genetics* **35**:485–490.

SHARON, N. and LIS, H. (1993): Carbohydrates in cell recognition. *Sci. Amer.* **268**:74–81.

SLATKIN, M. (1981): Populational heritability. *Evolution* **35**: 859–871.

SOBER, E. (1984): *The Nature of Selection, Evolutionary Theory in Philosophical Focus*. MIT Press, Cambridge.

SOBER, E. (1987): Comments on Maynard Smith. In DUPRÉ, J. (ed.): *The Latest on the Best, Essays on Evolution and Optimality*. MIT Press, Cambridge, pp. 133–149.

SOBER, E. and WILSON, D. S. (1994): A critical review of philosophical work on the units of selection problem. *Philosophy of Science* **61**:534–555.

SOBER, E. and WILSON, D. S. (1998): *Unto Others, The Evolution and Psychology of Unselfish Behavior*. Harvard University Press, Cambridge.

SZATHMÁRY, E. (1999a): The first replicators. In KELLER, L. (ed.): *Levels of Selection in Evolution*. Princeton University Press, Princeton, pp. 31–52.

SZATHMÁRY, E. (1999b): Chemes, genes, memes: A revised classification of replicators. *Lectures on Mathematics in the Life Sciences* **26**:1–10.

SZATHMÁRY, E. and MAYNARD SMITH, J. (1993): The origin of genetic systems. *Abstracta Botanica* **17**:197–206.

SZATHMÁRY, E. and MAYNARD SMITH, J. (1995): The major evolutionary transitions. *Nature* **374**:227–232.

SZATHMÁRY, E. and MAYNARD SMITH, J. (1997): From replicators to reproducers: The first major transitions leading to life. *J. Theor. Biol.* **187**:555–572.

VRBA, E. and GOULD, S. J. (1986): The hierarchical expansion of sorting and selection: Sorting and selection cannot be equated. *Paleobiology* **12**:217–228.

WADE, M. J. (1979): Sexual selection and variance in reproductive success. *Amer. Natur.* **114**:742–747.

WADE, M. J. (1996): Adaptation in subdivided populations: Kin selection and interdemic selection. In ROSE, M. and LAUDER, G. (eds): *Adaptation*. Academic Press, San Diego, pp. 381–405.

WADE, M. J. and KALISZ, S. (1990): The causes of natural selection. *Evolution* **44**:1947–1955.

WADE, M. J. and MCCAULEY, D. M. (1980): Group selection: The phenotypic and genotypic differentiation of small populations. *Evolution* **34**:799–812.

WILLIAMS, G. (1966): *Adaptation and Natural Selection*. Princeton University Press, Princeton.

WILSON, D. S. (1975): A theory of group selection. *PNAS* **72**:143–146.

WILSON, D. S. (1980): *The Natural Selection of Populations & Communities*. Benjamin/Cummings, Menlo Park.

WILSON, D. S. and DUGATKIN, L. (1997): Group selection and assortative interactions. *Amer. Natur.* **149**:336–351.

WILSON, D. S. and SOBER, E. (1994): Reintroducing group selection to the human behavioral sciences. *Behav. Brain Sci.* **17**:585–654.

WIMSATT, W. (1980): Reductionistic research strategies and their biases in the units of selection controversy. In NICKLES, T. (ed.): *Scientific Discovery, volume II: Historical and Scientific Case Studies*. D. Reidel, Dordrecht, pp. 213–259.

WIMSATT, W. (1981): Units of selection and the structure of the multilevel genome. In ASQUITH, P. and GIERE, R. (eds): *PSA 1980*. Volume 2, pp. 122–183.

WOODWARD, J. (1993): Capacities and invariance. In EARMAN, J., JANIS, A., MASSEY, G. and RESCHER, N. (eds): *Philosophical Problems of the Internal and External Worlds*. University of Pittsburgh Press, Pittsburgh, pp. 283–328.