The concepts of fitness and selection in evolutionary biology

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This paper examines the concepts of selection and fitness as they have been defined and used by various workers in evolutionary biology. In doing so, it presents several closely related versions of the theory of organic evolution.

The paper argues that the several concepts of selection are related in a fairly simple way. Some of the concepts are equivalent to each other and lead to equivalent formulations of the theory of organic evolution. Other concepts of selection are not equivalent to those in the first group. These non-equivalent concepts, however, lead to versions of the theory of evolution that are logically very close to the equivalent formulations of the theory.

The paper discusses four major definitions of fitness ('tautological' fitness, Darwinian fitness, Thodayan fitness and inclusive fitness), and presents the main properties of each. It is argued here that under each definition of fitness, fitness can be understood as a measure of the intensity of selection. This explains why the basic theory of organic evolution can be stated without mentioning fitness.

Finally, the question of whether the theory of organic evolution is 'tautological' is addressed. Many authors have thought that it is. If the accounts of selection, of fitness, and of the several versions of the theory of evolution here presented are even approximately correct, the theory of evolution is not the kind of thing that can be tautological. This is because it makes fairly straightforward existential claims and existential claims of the sort envisioned here cannot be tautological or analytic.

1. Introduction

There are at least two good reasons for studying the concept of fitness as it appears in evolutionary biology. First, the theory of evolution is central to all of biology and the concept of fitness has an important function in the application of the theory of evolution, if not within the theory itself. There is a problem, however, in that it is not at once obvious just in what the concept of fitness consists. Practicing evolutionists have complained that the concept lacks clarity or comprehensiveness. Hamilton (1964) writes that 'there does not seem to be any comprehensive definition of fitness.' He does not propose one. Kempthorne and Pollak (1970) complain that 'The mathematical literature of genetics refers to "fitness" very frequently without, in our opinion, a usable definition.' They do not propose one.

The problem of understanding what fitness is is compounded by the fact that it is difficult if not impossible to find a clear and succinct statement of the theory of evolution (this is so notwithstanding Mary Williams (1973) and elsewhere), and by the fact that 'fitness' appears to be used in a variety of ways. Even within the mathematical definitions of fitness, fitness can take on a series of different value ranges. Sometimes fitnesses range over the positive real numbers; sometimes over the reals between 0 and 1; sometimes over the reals greater than or equal to 1. (Also, different units are said to have fitnesses. These include genes, genotypes, individual organisms.) Part of the purpose of this paper is to describe the concept of fitness, actually the various concepts of

fitness, in such a way that usage of that term is seen to form a more or less coherent whole.

The second reason for studying the concept of fitness is that there has been a suspicion, often expressed, that the theory of organic evolution is in some way devoid of scientific, empirical content (see Barker, 1969; Flew, 1967; Hull, 1974; Manser, 1965; Peters, 1976; Scriven, 1959; Himmelfarb, 1962; Smart, 1963; Grene, 1974). The theory, as charged, is 'analytic' or 'tautological' or even 'almost tautological'. In what follows I examine these charges quite seriously and give a detailed response to them, but I do so without rehearsing the positions of those making the charge. I will present several versions of the theory of evolution, beginning with Darwin's and I will examine various definitions of fitness. At the end, it will be obvious whether and in what sense these charges are correct.

In presenting my findings I shall make three simplifying assumptions, any or all of which could be revoked without changing my conclusions. First, what little mathematic treatment I employ is rudimentary. For the sake of simplification I shall assume that populations are discrete (finite in size) and that generations are non-overlapping. In particular, I shall not discuss models using the Malthusian parameter. Fisher (1930), Haldane (1932), and Crow & Kimura (1970) give clear discussions of the Malthusian parameter. My adding a discussion of it would not greatly add to the substance of my findings.

My second simplifying assumption is that evolution, according to the synthetic theory, is coterminus with change of gene frequencies. In fact, it is not, change of gene frequencies being neither necessary nor sufficient for evolution. Not all units of heredity are genes (see Wright, 1969, chapter 6); some hereditary units being non-genic and extra-chromosomal. Genotype frequencies may change without gene frequencies changing, as in assortative mating, for example. Also, speciation may occur by chromosomal doubling (or trebling, etc.), which does not entail either a change in gene frequency or a change in genotype frequency. This second assumption is, however, a close approximation to what is thought to be the truth, most significant evolutionary events being thought to consist of changes in the frequencies of Mendelian genes.

The third assumption is a philosophical one. I shall assume that there is a proper distinction between statements that are analytically true (true in virtue of the meanings of their constituent words) and statements that are synthetically true (true, but true in virtue of the non-linguistic world). The charge, mentioned above, that the theory of evolution is a tautology is correctly expressed as a charge that the theory of evolution is analytically true. But this is a fine point which I shall mostly ignore, nothing of import turning upon it.

To repeat: these assumptions have been made for the purpose of simplifying the exposition and they could be withdrawn without substantially affecting my conclusions.

2. Darwin's theory of evolution

The essentials of Darwin's theory of evolution can be put perspicuously as three basic assertions conjoined with some assumptions. Darwin accepted, and

did not present much in the way of evidence for, the following rather un-exceptional facts:

(1) organisms are born and regularly succumb to death;

(2) organisms tend to reproduce;

(3) organisms tend to exhibit considerable adaptation to their natural environments;

(4) organisms tend to fit rather nicely into the standard taxonomic categories: varieties, species, genera, families, and so on.

These are Darwin's main assumptions, at least for the purpose of supporting his theory. That theory is, as the title of his book *(On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life)* indicates, a theory purporting to account for the origin of species. The three basic assertions of his theory are as follows.

(1) If there is variation in an interbreeding group of organisms; if there is variation which is heritable, at least to some degree; if not all individuals in the group can reproduce; and if, among the heritable variations which occur, some individuals possess traits which are of advantage for their survival and reproduction; then, with the passage of time, the interbreeding group will be modified, i.e., there will be descent with modification in the group.

(2) The antecedent conditions of (1) have been and are satisfied rather generally in natural and domestic populations, thus descent with modification has often occurred.

(3) Most of the world's present and past species and varieties have been formed by the process of descent with modification, as described in (1) and (2), above.

A few comments on these propositions are in order. First, Darwin did not speak of his theory as a theory of evolution. Rather, 'descent with modification by natural selection' was, repeatedly, his way of describing the theory. The process delineated in (1) is what he called natural selection. Selection occurs because not all individuals in the group can successfully reproduce, i.e. not every organism wins the 'struggle for existence'. The selection is natural because this process occurs without the intervention of any person. (In what follows, I shall not distinguish between natural and artificial selection but will simply speak of selection and its effects.)

This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. Variations neither useful nor injurious would not be affected by natural selection, and would be left a fluctuating element, as perhaps we see in the species called polymorphic (Darwin, 1859, p.81).

Proposition (1) is in the form of a conditional: if certain features obtain, then something will happen. Proposition (2) says that these features do in fact obtain. The following passage from the *Origin*, in which Darwin is summarizing his theory, shows clearly this structure in his theory.

If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organization, and I think this cannot be disputed; if there be, owing to the high geometrical powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to

be advantageous to them. I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals this characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterised. This principle of preservation, I have called, for the sake of brevity, Natural Selection (Darwin, 1859, pp. 126—127).

Proposition (3) is needed to complete the theory. Darwin thought not only that descent with modification by natural selection occurs (as shown by (1) and (2)), but that this process could account for the origin of species. It is not clear exactly how far Darwin wanted to push his evolutionism. He is committed to this theory for the origin of varieties and species. Oftentimes he pushes it to cover genera and families. At one point, he even speculated that all living forms are descended from a common ancestor.

I cannot doubt that the theory of descent with modification embraces all the members of the same class. I believe that animals have descended from at most only four or five progenitors, and plants from an equal or lesser number.

Analogy would lead me one step further, namely, to the belief that all animals and plants have descended from some one prototype. But analogy may be a deceitful guide. Nevertheless all living things have much in common, in their chemical composition, their germinal vesicles, their cellular structure, and their laws of growth and reproduction. We see this in so trifling a circumstance as that the same poison often similarly affects plants and animals; or that the poison secreted by the gall-fly produces monstrous growths on the wild rose or oak-tree. Therefore I should infer from analogy that probably all the organic beings which have ever lived on this earth have descended from some one primordial form, into which life was first breathed (Darwin, 1859, pp. 483—484).

This is, briefly, Darwin's theory of evolution. What else he has to say in the *Origin* can be understood mainly as evidence given in favor of the theory, as predictions and explanations made using the theory, response to objections to the theory, and comparison of the theory with the special creation theory.

Darwin did not originally use the term fitness in any technical sense. But the expression 'survival of the fittest' did come to his attention and he accepted it. At the beginning of his book, *The Variation of Animals and Plants under Domestication,* Darwin recounts his theory in much the way described above. He then defines natural selection and introduces the 'survival of the fittest' terminology:

This preservation, during the battle for life, of varieties which possess any advantage in structure, constitution, or instinct, I have called Natural Selection; and Mr. Herbert Spencer has well expressed the same idea by the Survival of the Fittest (Darwin, 1875, p. 6).

Thus, for Darwin, saying that species come about by natural selection and that species are created by survival of the fittest amounts to saying one and the same thing.

3. The synthetic theory of evolution

The modern, or synthetic, theory of evolution consists of a family of interrelated theories and theoretical concepts. These different versions and characterizations of the theory are related at least by the fact that they are

theories of organic evolution and by the fact that they attempt to integrate Darwinism and Mendelism into a coherent whole. In what follows I hope to present and discuss the central features of these various versions of the synthetic theory and to answer the questions posed at the beginning of the essay. In doing so, it will be useful to begin with what I shall call the classical versions of the theory.

Within the classical synthetic theory of evolution there are two main definitions, or characterizations, of selection. The following definition of selection is a reconstruction of one of these definitions.

DS-1. Selection occurs in a population if and only if in that population non-randomly differential reproduction of distinct genes occurs.

This is, I believe, a fair characterization of the position taken by a large number of authors. (The number is large, but see Crow (1958), Grant (1963, 1977) and Ayala (1975). Many authors are not explicit in excluding random effects, e.g., Wilson (1975) and Dobzhansky (1970). These authors are, however, concerned elsewhere to count random effects as things other than selection which can influence gene frequencies. I find this typical.) DS-1 is a definition of selection meant to capture the notion of genetic change brought about by what Darwin would call the 'preservation of favourable variations and the rejection of injurious variations', with the variants in this case being distinct genes. What changes, then, when evolution occurs is the genetic constitution of a population. Note that the second assumption of section 1, that evolution is co-extensive with change in gene frequency, is being brought into play here. It is possible for a population to be in genic equilibrium and for there to be differential mortality and fertility among genotypes, without gene frequencies changing. I am not considering this as evolution, because I want to simplify the presentation.

The requirement, in DS-1, that the differential reproduction be non-random amounts to a requirement that the reproductive success of a particular genotype not be a product of chance. In the same environment, selection acts equally on identical genotypes. If one of a pair of identical twins is struck by lightning, this is attributed to chance, not to selection being able to distinguish between genetically identical organisms.

It is obvious that DS-1 captures much of the spirit of Darwin's definition of natural selection. It also coheres well with that given by Sewall Wright (see also Wright, 1931, 1945, 1949*a,b*):

DS-2. Selection occurs in a population if and only if gene frequency is altered 'in a directed fashion without change of the genetic material (mutation) or introduction from without (immigration)' (Wright, 1969, p. 28).

Random effects are those which alter gene frequencies in a non-directed fashion. Both DS-1 and DS-2 explicitly exclude chance effects as factors in natural selection. What Wright has done is to define selection in terms of what it is not.

Directed changes are of three sorts — those due to recurrent mutation, to recurrent immigration, and to selection. The last is a wastebasket category that includes all causes of directed change that do not involve change of the genetic material or introduction from without (Wright, 1969, p. 473).

It is natural to ask whether DS-1 and DS-2 are equivalent definitions. The Appendix contains an argument that DS-1 and DS-2 are indeed equivalent.

With DS-1 and DS-2 as our definitions of selection, we can now construct the synthetic theory of organic evolution, or at least one version of it. This first version, Version A, consists of two definitions and three assertions, the three assertions being analogs to Darwin's first three assertions.

Version A of the Synthetic Theory

Definition 1. Evolution is change in gene (allele) frequency within a population.

Definition 2. DS-1 and/or DS-2.

(1) If selection occurs in a population and if its effects are not counterbalanced by mutation, immigration, and/or random effects, then evolution will occur by selection.

(2) Selection which is not completely counterbalanced by mutation, immigration, and/or random effects has often occurred and does often occur.

(3) Very much of organic evolution has been produced by selection. Species, in particular, have most often been produced by the effects of selection not completely counterbalanced by mutation, immigration, and/or random effects.

Version A, like the other versions to be discussed in what follows, should be understood as a reasonable approximation to the synthetic theory. The truth of (3) is problematic, depending upon which theory of speciation is correct (see Wright, 1949; Mayr, 1970; Grant, 1977; Dobzhansky, 1977; and many others).

If Version A is accepted as a good approximation of the synthetic theory, something definite can be said about the empirical status of the theory. (1) is clearly without empirical content; it follows from definitions and is true analytically. Not so for (2) and (3), which have the logical form of rather simple existential statements and so cannot be logically or analytically true. It is obvious that their truth, if they are true, is a straightforwardly empirical and scientific matter.

Wright's definition of selection, DS-2, rather obviously counts a large number of processes as components of selection. Selection can act in many ways and Wright is well aware of this (see also Crow & Kimura, 1970, p. 175).

As thus defined, selection includes many diverse processes. It includes gametic and zygotic selection or, in plants, gametophytic and sporophytic selection. It may depend on differences in mortality or in tendency to emigrate up to and in some cases beyond the reproductive age, on differences in onset and duration of reproductive capacity, on success in mating, and on fecundity (Wright, 1969, p. 29).

A number of authors have differed with Wright and have thought of meiotic drive not as a component of selection as does Wright (1969, p. 29), but as a distinct cause of change of gene frequencies, as are mutation and immigration (see Crow, 1979; Bossert & Wilson, 1971). This disagreement is easily accommodated by narrowing the definition of selection. The following is an analog of DS-1.

DS-3. Selection occurs in a population if and only if in that population non-randomly differential reproduction of distinct genes occurs and this differential reproduction is not caused by meiotic drive.

For present purposes, meiotic drive can be defined as any departure from Mendelian ratios of genes that is caused by meiotic events. The analog of DS-2 is:

DS-4. Selection occurs in a population if and only if gene frequency is altered in a directed fashion without change of the genetic material, introduction from without, or meiotic drive.

If DS-1 and DS-2 are equivalent, then so are DS-3 and DS-4. These latter definitions of selection lead to Version B of the synthetic theory.

Version B of the Synthetic Theory

Definition 1. As in Version A.
Definition 2. DS-3 and/or DS-4.
  (1) If selection occurs in a population and if its effects are not counter-balanced by mutation, immigration, random effects, and/or meiotic drive, then evolution will occur by selection.
  (2) Selection which is not completely counterbalanced by mutation, immigration, random effects, and/or meiotic drive has often occurred and does often occur.
  (3) Very much of organic evolution has been produced by selection. Species, in particular, have most often been produced by the effects of selection not completely counterbalanced by mutation, immigration, random effects, and/or meiotic drive.

DS-3 and DS-4 are narrower definitions of selection than are DS-1 and DS-2. Some authors have opted for a broader definition. Simpson (1953, p. 138) is an example.

I propose slightly to extend the definition used in population genetics and to define selection, a technical term in evolutionary studies, as *anything tending to produce systematic, heritable change in populations between one generation and the next.*

Reconstructing Simpson's definition, we have:

DS-5. Selection occurs in a population if and only if gene frequency is altered in a directed fashion.

Simpson's version of what selection is, as well as a whole host of different versions, can easily be accommodated by the synthetic theory through the device of developing Versions D,C,E, etc. in the way Version B was derived. As a result of these different definitions of selection, distinct but related versions of the synthetic theory of evolution arise.

It is interesting to note that Wright has given an argument against construing selection as in DS-5. Wright's argument (1955) is that whatever selection is, selection cannot change gene frequencies in a population unless there is more than one gene (or selection cannot change allele frequencies at a locus unless there is more than one allele present). Darwin (1859) also insisted on this. Mutation and immigration, however, are quite able to change allele frequencies

even if, in the population in question, only a single allele is present. Hence, selection does not include mutation or immigration.

Given any of the above versions of the synthetic theory of evolution, it becomes natural to develop a concept which measures the degree or intensity of selection. Fitness, selective value, or adaptive value is such a concept (see Haldane (1932), Li (1955) and also Maynard Smith (1976). This is not to deny that there may be other ways to measure the intensity of selection, e.g. Crow (1958, 1961).) In what follows I shall examine and compare the several definitions of fitness which have appeared prominently in the literature of evolutionary biology. Each of these concepts of fitness, I shall argue, is a measure of the degree or intensity of selection. They can conveniently be grouped in four categories and shall be so discussed (sections 4, 5, 6 and 7).

4. The 'tautological' definition of fitness

As noted in the first section of this paper, a number of authors, among them both practicing biologists and commenting philosophers, have understood the assertion 'The fittest survive' (and similar assertions) as analytically true ('tautological') and hence trivially true *a priori*. Part of the purpose of this section is to elucidate how and in what sense this is right, or can be right.

One way to define fitness is simply in terms of survival. Those organisms which survive are, by this definition, the fittest. To say, then, that the fittest survive is to repeat a definition. Several important evolutionists define fitness in just this way (e.g. Wilson, 1975). The following comments are typical.

It is unfortunate that Herbert Spencer proposed the expression "survival of the fittest" for Darwin's very apt term "natural selection," and that Spencer's expression was accepted even by Darwin himself, as well as by many others, as equivalent to Darwin's own. For the word "fittest" in Spencer's phrase can only be properly defined as meaning: "having such a character as better to survive." Thus his expression, taken literally, must be translated as reading: "the survival of those which survive." This tautological form has led to people into philosophical muddles and has caused them even to question the validity of the entire concept (Muller, 1949).

The meaning of natural selection (sic) can be epigrammatically summarized as 'the survival of the fittest'. Here 'suvival' does not, of course, mean the bodily endurance of a single individual, outlining Methuselah. It implies, in its present-day interpretation, perpetuation as a source for future generations. That individual 'survives' best which leaves the most offspring. Again, to speak of an animal as 'fittest' does not necessarily imply that it is strongest, or most healthy, or would win a beauty competition. Essentially it denotes nothing more than leaving most offspring. The general principle of natural selection, in fact, merely amounts to the statement that the individuals which leave most offspring are those which leave most offspring. It is a tautology. It is only when we penetrate beyond the field of generalities, to consider what different kinds of selection might be expected to occur, that we pass out of the sphere of empty truisms into the region where empirical scientific investigation is possible (Waddington, 1957, pp. 64–65).

Ayala, although he disagrees with it, has described a similar view.

Critics accusing the theory of natural selection of circularity generally refer to circularity of argumentation. They believe that arguments of natural selection proceed approximately as follows. Natural selection occurs whenever two or more alternative genetic variants have difference "fitnesses" or "adaptive values" in a given environment; variants with higher fitnesses will increase in frequency over the generations at the expense of the variants having

lower fitnesses.... Now, which genetic variants have higher fitness? Simply, those whose carriers reproduce more effectively. The conclusion that some genetic variants increase, and others decrease, in frequency is used in the premises in order to define the "fitnesses" (Ayala, 1975, pp. 21, 22).

Muller, Waddington and Ayala were or are practicing biologists, but a number of philosophers have given similar descriptions of the notion of fitness. (See Barker, 1969; Flew, 1967; Hull, 1974; Manser, 1965; Peters, 1976; Scriven, 1959; Himmelfarb, 1962; Smart, 1963; Grene, 1974.)

Several comments are in order. The picture of the theory of evolution which emerges from these authors is somewhat different than any of Versions A, B or (implicitly) C. These authors describe a view in which selection is just any differential reproduction and fitness is just actual reproductive success. Rather obviously, this view can be expressed as in section 3. We now have a sixth definition of selection.

DS-6. Selection occurs in a population if and only if gene frequency is altered.

This is perhaps the broadest definition of selection possible, broader even than Simpson's (DS-5). Its corresponding version of the theory of evolution is Version D.

Version D of the Synthetic Theory

Definition 1. As in Version A.
Definition 2. DS-6.
  (1) If selection occurs in a population, then evolution will occur by selection in that population.
  (2) Selection, other than that due to mutation, immigration, and random effects, has often occurred and does often occur.
  (3) Very much of organic evolution has been produced by selection other than that due to mutation, immigration, and random effects. Species, in particular, have most often been produced by the effects of such selection.

The 'tautological' definition of fitness (i.e. that the fittest are those organisms which survive) goes with Version D of the synthetic theory of evolution. Note, however, that while 'The fittest survive' is analytic (or tautological), the theory, Version D, is not at all empirically empty. Like (1) of Version A, (1) of Version D is a definitional truth and is empirically empty. Also like (2) and (3) of Version A, (2) and (3) of Version D are clearly not candidates for empirical vacuity. Their truth values can be determined only scientifically. Thus, even Version D is not an empirically empty theory.

The 'tautological' definition of fitness is not the most widely accepted and used characterization of fitness. There seem to be at least three reasons why. First, under the tautological definition, genetically identical individuals need not have identical fitnesses in the same environment. For example, given two identical twins, S and T, if S is accidentally killed before the age of reproduction and T survives to produce a large number of offspring, then T's fitness is much higher than S's. This is generally thought to be somewhat anomalous.

A second difficulty with the tautological definition of fitness is that its

attendant definition of selection implies that all evolution is by selection and this does not permit sensible discussion of evolution by mutation, drift, etc., opposing evolution by natural selection. Very many authorities on evolution are wont to put matters this way, including any authors using the concept of Darwinian fitness (section 5), including Fisher, Haldane and Wright. (See also King and Jukes (1969).)

A third difficulty arises as a result of an argument presented by Wright (1955), who notes that selection, as usually understood, cannot change gene frequencies when there is only one type of gene. This argument was discussed at the end of section 3.

The tautological definition of fitness is, it should be noted, open to quantification. The fitness of an individual is the number of progeny it leaves divided by the number of parents it took to leave a typical offspring. Here, 'individual' can be understood in any of several senses: an individual organism, an individual genotype, and individual allele, etc. The relative fitness of an individual is the relative success it has in leaving progeny, compared with the other individuals in its population. Because the tautological definition of fitness can be so quantified, it is possible to interpret certain equations employed mainly with Darwinian fitness (discussed in section 5) as describing what happens under a description of tautological fitness. We shall return to this subject in the section following.

Finally, when quantified, the tautological definition of fitness can be understood as a measure of selection as defined by DS-6. The relative fitness of an individual is its relative selective advantage (or disadvantage). How much has selection operated on a particular individual? Compare its (relative or absolute) fitness with the fitness of the other individuals constituting the population in question.

5. Darwinian fitness

The term Darwinian fitness is used in the primary literature of evolutionary biology in several different senses, including that which I shall use. As I refer to it, Darwinian fitness is the most frequently used sense of fitness. It subsumes a large number of definitions having in common the fact that they define fitness (implicitly or explicitly) as an expectation of progeny. This can be done in an absolute or in a relative fashion, as we shall see. The definition of absolute Darwinian fitness is examined first.

Waddington's characterization of fitness as 'the capacity to contribute offspring to the next generation' (1957, p. 109) is a standard conception of fitness which is explicated by defining fitness, in the absolute sense, as an expectation. Crow & Kimura define it as follows:

We define fitness, or selective value, as the expected number of progeny per parent. The parents and progeny must be counted at the same age, of course. The effects of differential mortality and fertility are kept within the same generation if each generation is enumerated at the zygote state. In a biparental population, half of the progeny are credited to each parent (Crow & Kimura, 1970, p. 178).

Letting W stand for fitness, then we have:

$$W = df \sum_{i=0}^{\infty} (p_i)(i)/2 \tag{1}$$

for a biparental population. Here, i is the number of progeny and p_i is the probability of having i progeny. Many authors refer to fitness as the average number of progeny per parent, but of course this amounts to the same thing as the expected value. These authors include Ayala (1975), Crow (1958, 1961), Crow & Nagylaki (1976), Dawkins (1976), Kempthorne & Pollak (1970) and Slatkin (1978). Fisher (1930, p. 25) was perhaps the first to call fitness an 'expectation of offspring'.

Before discussing relative fitness, there are a number of important points to be noted about absolute Darwinian fitness.

1. . Absolute Darwinian fitness is a magnitude with dimensions (*progeny per parent*). This magnitude can take on real values from zero to plus infinity.
2. Although (1) defines fitness in an absolute sense, W must still be understood to be relativized to a particular environment at a particular time. The various p_i's should be taken to be conditioned upon a particular (but seldom specified) environment and time.
3. Definition (1) does not specify what has fitness, i.e. whether it is individual organisms, particular alleles, genotypes, or whatever. How it is that selection acts is a matter of controversy and a matter of controversy beyond the ken of this essay. (See Fisher, 1930; Crow & Kimura, 1970; Wright, 1943; Dawkins, 1976; Grant, 1963; Lewontin, 1970; Mayr, 1970; Maynard Smith, 1975, 1976, 1978; Williams, 1971, 1966; and anything on inclusive fitness (section 7).) By use of subscripts standing for alleles, genotypes, individual organisms, and so on, we can maintain (with neutrality to the question of the level of selection) this definition of fitness and thereby apply it to different biological units.

   As an example, we could, with Wright (1931, p. 101), hold that 'Selection, whether in mortality, mating or fecundity, applies to the organism as a whole and thus to the effects of the entire gene system rather than to single genes'. Given this it remains possible to talk of the fitness of a single gene or of the fitness of a genotype at a particular locus. There are two ways this might be done. One could, as Wright does, think of the fitness of an allele as merely a useful approximation.

The selection coefficient for a gene is thus in general a function of the entire system of gene frequencies. As a first approximation, relating to a given population at a given moment, one may, however, assume a constant net selection coefficient for each gene (Wright, 1931, p. 101).

A second alternative would be to follow Crow & Kimura (1970, see p. 180) and to interpret W_x, the absolute fitness of the allele x, as the average fitness of all genotypes in the population containing allele x. Similar moves can be made with respect to the fitness of a particular genotype.

4. Fitness defined in (1) is a measure of the intensity of selection, defined as in DS-1 (section 3). The fitness of an individual, defined by (1) is the amount of non-random reproduction it has undergone. The expected, or average, value of the progeny is just the number of progeny per parent which there would be if random effects were excluded. Thus, by comparing the various absolute fitnesses in a population the comparative degree to which selection is operating can be measured.

5. The absolute Darwinian fitness is not identified with the actual number of progeny per parent, but with the expected number of progeny, a quantity that is only estimated by the actual number of progeny. Herein lies, perhaps, a main difficulty with this notion of fitness: it is difficult to measure. There have been various attempts to measure fitness and these can be consulted on the difficulty of obtaining a good estimate of actual fitness (Knight & Robertson, 1957; Li, 1955; Prout, 1965).

6. Unlike the tautological definition of fitness, genetically identical individuals do have identical Darwinian fitnesses. The twin killed accidentally has exactly the same fitness as the twin which reproduced extensively.

7. High fitness does not guarantee evolutionary success. This is true for several reasons, among them the following.

    (a) As we have seen, an individual with high fitness may, due to an accident fail to reproduce and hence leave no descendents.

    (b) Fitness is defined only over one generation. The environment may change with time and .in subsequent generations what was once highly fit may no longer be so.

    (c) Because fitness is defined (here) only over one generation, a gene may be selected for, which in later generations causes its bearers to have much lowered fitness, even in the case of no environmental change. An example is the *grandchildless* gene in *Drosophila,* which gives its bearers increased fitness, but the progeny in the next generation are sterile. Haldane gives a second example:

Clearly a higher plant species is at the mercy of its pollen grains. A gene which greatly accelerates pollen tube growth will spread through a species if it causes moderately disadvantageous changes in the adult plant. A gene producing changes which would be valuable in the adult will be unable to spread through a community if it slows down pollen tube growth (Haldane, 1932, p. 123).

And there are other examples (e.g. Crow, 1979).

8. As Crow & Kimura note, 'the ways that selection can opeate are uncountable'. W, defined by (1), is a measure of the total effect of selection. It is possible, then, to partition fitness into any number of exhaustive and mutually exclusive elements. A common way in which this is done is to partion fitness into viability and fertility. Let:

v_{ij} = the probability that genotype $A_i A_j$ survives to the age of reproduction;

f_{ij} = the expected number of progeny of genotype $A_i A_j$, given that it survives to the age of reproduction;

w_{ij} = the absolute Darwinian fitness (defined in (1) above) of genotype $A_i A_j$.

Then, $W_{ij} = v_{ij} f_{ij}$. See Crow & Kimura (1970, p. 185) and Kempthorne & Pollak (1970) for further discussion of this method.

So far in this section we have considered only absolute Darwinian fitness; we now turn to relative Darwinian fitness, which is employed perhaps even more frequently than fitness in the absolute sense. A very small sample is: Wright (1931 and later); Crow & Kimura (1970); Crow elsewhere; Demetrius

(1977); Dobzhansky (1968, 1970, 1977); Falconer (1960); Grant (1963, 1977); Lewontin (1974); Li (1955); Maynard Smith (1975); Verner (1977); and textbooks everywhere. Relative fitness can be thought of as a ratio of absolute fitnesses. Allow that we are concerned with the fitnesses of several genotypes at a single locus. We choose the absolute fitness of one of the genotypes as our standard. The relative fitness of a genotype is then the ratio of its absolute fitness to the absolute fitness of the standard. The relative fitness of the standard genotype is, by this method, always equal to 1.

Table 1 provides an illustration of this method. In this example the genotype with the higher fitness, A_1A_1, is taken as the standard. Given this, w_{22} can be understood as the product of w_{11} (=1) and a factor which is less than one. A convenient expression for this factor is $(1-s)$, where s is called (after Wright (1931 and elsewhere)) the coefficient of selection. Thus, we have

$$w_{22} = w_{11}(1-s) = (1-s)$$

because w_{11} is equal to 1. The relative fitness of the heterozygote, A_1A_2, can be similarly treated. In this case, however, it is customary to give the relative fitness of A_1A_2 as $(1-hs)$, where s has the value it has in the expression for w_{22} and h is a measure of any dominance effect. Note that in this case the relative fitnesses range from 0 to 1, as does s.

Table 1

Genotype	A_1A_1	A_1A_2	A_2A_2
Absolute fitness	w_{11}	w_{12}	w_{22}
Relative fitness	$w_{11} =$	$w_{12} =$	$w_{22} =$
	W_{11}/W_{11}	W_{12}/W_{11}	W_{22}/W_{11}
	$= 1$	$= (1-hs)$	$= (1-s)$

There is, of course, more than one way to choose the standard when determining relative fitnesses. Any genotype present can be chosen as the standard. When genotypes other than that with maximal absolute fitness are chosen, different values of the relative fitnesses are possible. For example, if the genotype with the lowest (but non-zero) absolute fitness is chosen as the standard, the values for the relative fitnesses range from 1 to positive infinity. If a genotype with an intermediate-valued absolute fitness is chosen as the standard, the relative fitnesses range over the positive real numbers.

As in the case of absolute Darwinian fitness, there are a number of points to be made about relative Darwinian fitness.

1. Relative Darwinian fitness is a magnitude without a dimension. This is because it is a ratio of two magnitudes with identical dimensions and the dimensions cancel.

2. Like absolute fitness, relative fitness must be understood as relativized to a particular environment at a particular time.

3. As in the case of absolute fitness, genes, genotypes, individual organisms, and so on can be understood to have relative fitnesses.

4. Relative fitness is a measure of the intensity of selection; it indicates change due to selection. As an illustration, consider Table 2. There, it is assumed

Table 2

Genotype	A_1A_1	A_1A_2	A_2A_2
Relative fitness	1	1	$(1\text{-}s)$
Initial frequency	p^2	$2pq$	q^2
Gametic contribution (Relative Fitness. Initial frequency)	p^2	$2pq$	$q^2(1\text{-}s)$

The initial frequency of allele A_2 is $q \times$ The frequency of A_2 in the next generation, q_1, is:

$$q_1 = \frac{q^2(1\text{-}s) + pq}{1 - sq^2} \quad .$$

The change in the frequency of A_2 is:

$$\triangle A_2 = q_1 - q = \frac{\text{-}sq^2(1\text{-}q)}{1 - sq^2} \quad .$$

that h is zero (no dominance). The equations for the change in the frequency of the A allele assume that random effects, mutation and immigration are not present. If the fitnesses are interpreted as relative Darwinian fitnesses, these equations describe the change in the frequency of the A allele which would occur if no factors other than selection (DS-1) were present changing the gene frequencies. As noted at the end of section 4, the fitnesses could be (but seldom if ever are) interpreted in the tautological sense. In this case, the equations describe the change in the frequency of the A allele due to all possible causes and they are rather trivially true.

5. Points 5, 6, 7 and 8 applied above to absolute fitness apply also to relative fitnesses.

Finally, it should be noted that absolute and relative fitnesses may under certain conditions be misleading indicators of the effects of selection. The most successful genotype in a population which is rapidly going extinct may have a relative fitness of 1. Conversely, the least successful genotype in a population which is growing rapidly may have a fairly high absolute fitness. In both cases the genotype in question is heading for loss.

6. Fitness as persistence

Thoday (1953) has proposed a definition of fitness quite distinct from any of those so far examined in that Thoday's definition counts descendants not in the next generation, but in some temporally distant generation. His definition is as follows.

The fitness of a unit of evolution is by definition the probability that descendants of that unit will exist after a suitably long time, e.g., 10^8 years (Thoday, 1953, p. 98, my paraphrase).

Thoday has this to say about the unit of evolution and why he wants to define fitness as he does.

... the fitness of a group must include its capacity for future survival in future environments. We cannot, therefore, discuss directly the fitness of individuals or populations or species, for

to do so we should have to put entirley arbitrary limits on the time during which survival is to occur. If we are not so to limit this time, then the fitness of contemporary individuals or populations cannot be defined without reference to their offspring. Therefore the fitness of each generation is dependent to some measure on the mates of its descendants and we are forced to define fitness for survival in relation to that contemporary group of individuals which will sometime in the future have common descendants. These we .may call the contemporary representatives of a unit of evolutionary continuity or for the sake of brevity a unit of evolution.

It is, of course, well-nigh impossible to determine just where the boundaries of such a unit lie, because of the variation and variability of breeding structures. Where isolating barriers may in the future break down, where introgressive hybridization may occur, or where allopolyploids may arise, the unit of evolution must comprise more than one taxonomic species and often more than one biological species. On the other hand, where sexual reproduction has been permanently lost the representative at any one time of a unit of evolution must be an individual. There are all possible intermediate conditions (Thoday, 1953, p. 97).

Thoday is well aware that other definitions of fitness exist. He offered the present one not to overthrow the other concepts of fitness but to serve in his explication of biological progress. In the 1953 paper, Thoday argues that all and only progressive evolutionary changes increase fitness as he has defined it. With this in mind, it should be clear that Thoday's definition does not require any theory of evolution in addition to those already discussed. Thoday's definition of fitness is consistent with each of the versions of the theory of evolution.

Fitness as defined by Thoday has been discussed but not widely accepted. The general criticism has been that Thodayan fitness is an interesting but not very useful concept. The following comments are typical.

For the purpose of a purely formal theory, fitness can be given a simple definition, as the capacity to contribute offspring to the next generation. Thoday has suggested that it should be defined with reference to a longer lapse of time; . . . This is, as he shows, an interesting concept to discuss, but it is not what is usually meant by fitness in evolutionary theory, and it cannot replace the more conventional notion which is concerned only with the next generation. It is the latter which determines what evolutionary changes will happen here and now. Thoday's concept involves a notion similar to action at a distance; it is not a casual concept, since the Thodayan fitness of an individual existing now would be altered if some unforeseen of unforeseeable climatic change occurs even many years after it is dead (Waddington, 1957, pp. 109–110).

It may be doubted whether Waddington's charge that Thodayan fitness 'involves a notion similar to action at a distance' is really apt. First, fitness applies, for Thoday, to units of evolution and not generally to individual organisms, as Waddington suggests. Second, the probability of long term survival for a unit of evolution is conditioned upon the state of the contemporaneous world (Thoday, 1970). Thus, for example, if the Thodayan fitness of a unit of evolution is 0.97 at t_0 and if a million years later an earthquake destroys all the descendants of the unit, then the fitness at t_0 is unaltered. The probability of drawing a royal flush in poker is not altered by drawing a royal flush. The problem, however, with Thoday's concept is evident here. It is in practice difficult, if not impossible, to obtain a probability estimate of the significant events which might impinge upon the survivability of a unit of evolution. Dobzhansky and Ayala make just this criticism of Thoday's definition.

Fitness in Thoday's sense is evidently nor identical with either adaptedness or Darwinian fitness. It may perhaps be referred to as persistence. To be operationally useful, adaptedness and Darwinian fitness must explicitly refer to the time and to the environment, or the range of environments, when and where they are measured. The evolutionary persistence is operationally elusive; it depends on the countless contingencies which a species or a population will be facing in the future, and Thoday specifies a remote future, such as 10^8 years! At least given the present level of knowledge and techniques, there seems little chance of predicting the course of evolution even over time inte vals some orders of magnitude smaller than indicated by Thoday (Dobzhansky, 1968).

Thoday has enumerated a variety of components which contribute to the fitness of a population as defined by him. These components are adaptation, genetic stability, genetic flexibility, phenotypic flexibility and the stability of the environment. But it is by no means clear how these components could be quanitifed, nor by what sort of function they could be integrated into a single parameter. In any case, there seems to be no conceivable way in which the appropriate observations and measurements could be made for the ancestral population. Thoday's definition of progress is extremely ingenious, but lacks operational validity. If we accept his definition there seems to be no way in which we could ascertain whether progress has occurred in any one line of descent or in the evolution of life as a whole (Ayala, 1974, p. 344).

There are several more or less distinct and interesting features of Thoday's definition of fitness.

1. Like the other definitions of fitness, Thoday's is a measure of the intensity of natural selection. Darwinian fitness measures selection over one generation, Thodayan fitness over 10^8 years.

2. Given Thoday's definition, it does not follow that anything living before 10^8 years ago with descendents alive today has the maximum possible fitness. As argued above, actual survival does not affect the probability that the unit would survive.

3. Unlike the tautological definition of fitness, Darwinian fitness, and inclusive fitness (to follow), Thodayan fitness is a probability. As such it is fairly insensitive to the degree of survival. A unit with one descendant after 10^8 years could have the same Thodayan fitness as a unit with 10^{10} descendents. More precisely, consider two Thodayan units, U_1 and U_2. Let the probability that U_1 has one descendant after 10^8 years to be $1 \cdot 0$ and the probability that it has any other number of descendants after 10^8 years to be zero. Similarly, let the probability that U_2 has 10^{10} descendants after 10^8 years be 1.0 and the probability that it has any other number of descendants be zero. Then U_1 and U_2 have identical Thodayan fitnesses.

4. It would be possible to define a version of Darwinian fitness over more than one generation, but the result would still be an expectation not a probability (e.g. Verner, 1977; Demetrius, 1977).

In summary, whatever the merits of Thoday's definition it has not been widely accepted, it is not theoretically inconsistent with Darwinian fitness, and it, too, is a measure of the intensity of selection.

7. Inclusive fitness

A formal, extended account of inclusive fitness is beyond the scope of the present essay. Giving an informal description of inclusive fitness is, however,

fairly easy. Inclusive, or extended, fitness is similar to Darwinian fitness as discussed in section 5. Both concepts are defined in terms of the individuals constituting the succeeding generation. Whereas Darwinian fitness counts the progeny of an individual, inclusive fitness counts the progeny per parent *plus* relatives weighted by their coefficient of relation. (See Wright (1969), Crow & Kimura (1970) and Hamilton (1964) for the coefficient of relationship.)

Hamilton (1964) has developed the notion of inclusive fitness extensively, although his formal models which use it are not entirely general. His definition is as follows. Here 'fitness' by itself means what I have called Darwinian fitness.

Inclusive fitness may be imagined as the personal fitness (i.e Darwinian fitness) which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quanities of harm and benefit which the individual himself causes to the fitness of his neighbors. The fractions in question are simply the coefficients of relationship appropriate to the neighbors whom he affects; unity for clonal individuals, one-half for sibs, one-quarter for half-sibs, one-eighth for cousins . . . and finally zero for all neighbors whose relationship can be considered negligibly small (Hamilton, 1964).

The original notion of extended fitness appears in Fisher (1930) and Haldane (1932), and is discussed by Hamilton (1964). The introduction of inclusive fitness was motivated by the desire to understand certain natural phenomena. Both Fisher and Hamilton discuss the case of the evolution of insects which are distasteful to their predators. If fitness is understood in the Darwinian sense, it is difficult to see how such an adaptation might evolve. There does not appear to be any advantage to the individual in carrying an allele which makes its bearer distasteful. The predator will only avoid the insect after the predator has experienced the foul taste, but by then it is too late for the individual carrying the allele responsible for the taste. Fisher's treatment of the subject is worth repeating.

An important question raised by both the Batesian and the Mullerian theories of mimicry concerns the process by which nauseous flavours, as a means of defence, have been evolved. Most other means of defence such as strings, or disagreeable secretions and odours, are explicable by increasing the chance of life of the individuals in which they are best developed, or of the social community to which they belong. With distastefulness, however, although it is obviously capable of giving protection to the species as a whole, through its effect upon the instinctive or aquired responses of predators, yet since any individual tasted would seem almost bound to perish, it is difficult to perceive how individual increments of the distasteful quality, beyond the average level of the species, could confer any individual advantage (Fisher, 1930, pp. 177–8).

'The gregarious habit of certain larvae supplies', Fisher continues

a possible solution to the problem. . . with gregarious larvae the effect (of a predator eating a distasteful individual) will certainly be to give the increased protection especially to one particular group of larvae, probably brothers and sisters of the individual attacked. The selective potency of the avoidance of brothers will of course be only half as great as if the individual itself were protected; against this is to be set the fact that is applies to the whole of a possibly numerous brood. There is this no doubt of the real efficacy of this form of selection though it may well be doubted if all cases of insect distastefulness can be explained by the same principle (Fisher, 1930, p. 178).

Hamilton has developed this line of thought into a fairly general theory of social behaviour.

In brief outline, the theory (produced as a result of developing the notion of inclusive fitness) points out that for a gene to receive positive selection it is not necessarily enough that it should increase the fitness (in the Darwinian sense) of its bearer above the average if this tends to be done at the heavy expense of related individuals, because relatives, on account of their common ancestry, tend to carry replicas of the same gene; and conversely that a gene may receive positive selection even though disadvantageous to its bearers if it causes them to confer sufficiently large advantages on relatives (Hamilton, 1964).

Inclusive fitness has been pulled into service to explain social phenomena by a growing number of authors (e.g., Wilson, 1975; Trivers, 1972; Alexander, 1974; Hutchinson, 1978) and appears to be gaining wide acceptance (see Cassidy (1978) for a review). The concept has not, however, gone without criticism (see Wade, 1978).

For the present essay, inclusive fitness is similar to Darwinian fitness, and what was said about the latter can be said about the former. Both can be understood as expectations and both are measures of the intensity of selection.

8. Conclusions

In addition to Darwin's theory of evolution, we have examined four versions (A through D, C implicitly) of the synthetic theory of evolution, we have seen how other versions could be constructed, and we have examined a number of definitions of fitness. If what has been presented so far is accepted, the various definitions of fitness and selection are seen to fit into a rather coherent pattern, described above. In addition, there are four main results which fall out of this study.

1. It is evident that no version of the theory of evolution here discussed, including Darwin's, is analytic or in any way empirically empty. Within each version of the theory there is the claim that speciation has come about largely because of selection, when mutation, immigration, and random effects are excluded. This is a straightforwardly scientific, empirical, and possibly false assertion. It is certainly not true by definition.

2. The theory of evolution can be stated without reference to fitness or any cognate of that term. There is a sense in which 'fitness' and 'natural selection' may be interdefinable, but this is irrelevant to stating the basic theory of evolution. At the very least, while it may be possible to state a defensible and analytic version of the theory of evolution (although I doubt it), it is possible to state a defensibly non-analytic version of the theory.

3. In each case, fitness was a measure of selection. Also, different theories require different measures of selection, and there is more than one way to measure selection, even given a single version of the theory.

4. Finally, Versions A, C and D are, as presented, logically equivalent. That is, if one is true, they all are true; if one is false, they all are false. This is shown by the following considerations. Each version of the theory consists of two definitions followed by three assertions. Each pair of definitions should be taken as true, i.e. as true by definition. Assertion (1) of each version is a definitional truth (i.e. is analytic), given the definition of selection operating in that version of the theory. Also, assertions (2) and (3) of each version say the same thing, once the local definition of selection is taken into account.

Version B implies the other versions, because they do not rule out the possibility that meiotic drive is responsible for a large amount of evolution. This represents no great theoretical difference between the several versions. A, C and D could each be modified easily and made logiclaly equivalent to B.

It is, of course, possible to reject all of the versions of the synthetic theory which I have presented. One plausible reason why one might want to do this is that assertion (3) may seem false, or at least too restrictive. Wright has made the following comment.

The view that these species differences are largely due to mutations that were not only adaptive from the first but were carried directly to fixation by favourable selection is undoubtedly too simple, as indeed has probably been recognized in some degree by all who accept the general hypothesis of transformation (of species). It makes the occurrence of adaptive mutations the limiting factor in evolution to an extent that severely restricts the possible rate of evolutionary change, There is evidence that evolution can proceed with great rapidity, given an adequate ecological opportunity (Wright, 1949*a*, p. 367).

The issue here is a scientific one. Just what roles do selection and random effects play in speciation? The versions I have presented come down in favour of natural selection, but that is immaterial for my general point. The four versions are meant as approximations. If Version A is altered to reflect a greater role for chance in speciation, then so can Versions B, C, etc. My claim is that while there are different notions of what counts as selection, these different notions need not be committed to different theories of evolution.

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References

Alexander, R. D. (1974). *Ann. Rev. Ecol. Syst.* 5, 325.
Ayala, F. J. (1974). *Studies in the Philosophy of Biology* (Ayala & Dobzhansky, Eds). Berkeley: University of California Press.
Ayala, F. J. (1975). *The Role of Natural Selection in Human Evolution* (F. M. Salzano, Ed.). North-Holland Publishing Company.
Barker, A. D. (1969). *Philosophy* 44, 271.
Cassidy, J. (1978). *Philos. Sci.* 45, 575.
Crow, J. F. (1958). *Human Biol.* 30, 1.
Crow, J. F. (1961*a*) *Human Gen.* 13, 137.
Crow, J. F. (1961*b*). *Daedalus* (Summer), 416.
Crow, J. F. (1979). *Scient. Am.* 240, 134.
Crow, J. F. & Kimura, M. (1970). *An Introduction to Population Genetics Theory*. New York: Harper & Row.
Crow, J. F. & Nagylaki, T. (1976). *Am. Nat.* 110, 207.
Darwin, C. (1964). *On the Origin of Species: A Facsimile of the First Edition* (1859). Cambridge: Harvard University Press.
Darwin, C. (1875). *The Variation of Animals and Plants under Domestication*. London: John Murray.
Dawkins, R. (1976) *The Selfish Gene*. New York: Oxford University Press.
Demetrius, L. (1977). *Am. Nat.* 111, 1163.
Dobzhansky, T. (1968). *Population Biology and Evolution* (R. C. Lewontin, Ed.). Syracuse: Syracuse University Press.

Dobzhansky, T. (1970). *Genetics of the Evolutionary Process.* New York: Columbia University Press.

Dobzhansky, T. (1977). *Evolution.* San Francisco: W. H. Freeman.

Falconer, D. C. (1960). *Introduction to Quantitative Genetics.* New York: The Ronald Press Company.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection.* New York: Dover Publications, Inc. (reprinted 1958).

Flew, A. (1967). *Evolutionary Ethics.* New York: St. Martin's Press.

Grant, V. (1963). *The Origin of Adaptations.* New York: Columbia University Press.

Grant, V. (1977). *Organismic Evolution.* San Francisco: W. H. Freeman.

Grene, M. (1964). *The Understanding of Nature. Essays in the Philosophy of Biology.* Boston: D. Reidel.

Haldane, J. B. S. (1932). *The Causes of Evolution.* Ithaca: Cornell University Press (reprinted 1966).

Hamilton, W. D. (1964). *J. Theor. Biol.* **7**, 1.

Himmelfarb, G. (1963). *Darwin and the Darwinian Revolution.* New York: Doubleday.

Hull, D. (1974). *Philosophy of Biological Science.* Englewood Cliffs, N.J: Prentice-Hall, Inc.

Hutchinson, G. E. (1978). *An Introduction to Population Ecology.* New Haven: Yale University Press.

Kempthorne, O. & Pollak, E. (1970). *Genetics* **64**, 125.

King, J. L. & Jukes, T. H. (1969). *Science* **164**, 788.

Knight, G. R. & Robertson, A. (1957). *Genetics* **42**, 524.

Lewontin, R. C. (1970). *Ann. Rev. Ecol. Syst.* **1**, 1.

Lewontin, R. C. (1974). *The Genetic Basic of Evolutionary Change.* New York: Columbia University Press.

Li, C. C. (1955). *Population Genetics.* Chicago: The University of Chicago Press.

Li, C. C. (1955). *Am. Nat.* **89**, 281.

Manser, A. R. (1965). *Philosophy* **40**, 18.

Maynard Smith, J. (1975). *The Theory of Evolution,* 3rd ed. Hardmondsworth, England: Penguin.

Maynard Smith, J. (1976). *Am. Nat.* **110**, 331.

Maynard Smith, J. (1978). *The Evolution of Sex.* Cambridge: Cambridge University Press.

Mayr, E. (1970). *Populations, Species, and Evolution.* Cambridge: The Bellknap Press.

Muller, H. J. (1949). *Proc. Am. Phil. Soc.* **93**, 459.

Peters, R. H. (1976). *Am. Nat.* **110**, 1.

Prout, T. (1965). *Evolution* **19**, 546.

Scriven, M. (1959). *Science* **130**, 477.

Simpson, G. G. (1953). *The Major Features of Evolution.* New York: Simon and Schuster.

Slatkin, M. (1978). *Am. Nat.* **112**, 845.

Smart, J. J. C. (1963). *Philosophy and Scientific Realism.* New York: The Humanities Press.

Thoday, J. M. (1953). *Symp. Soc. Exp. Biol.* **7**, 96.

Thoday, J. M. (1970). *Can. J. Gen. Cytol.* **12**, 674.

Trivers, R. L. (1972). *Sexual Selection and the Descent of Man, 1871 –1971* (Campbell, B., Ed).

Verner, J. (1977). *Am. Nat.* **111**, 769.

Waddington, C. H. (1957). *The Strategy of the Genes.* New York: Macmillan.

Wade, M. J. (1978). *Evolution,* **32**, 220.

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

Williams, G. C. (Ed.) (1971). *Group Selection.* Chicago: Aldine, Atherton, Inc.

Williams, M. B. (1973). The Methodological Unity of Science (M. Bunge, Ed). Dordrecht: D. Reidel.

Wilson, E. O. (1975). *Sociobiology: The New Synthesis.* Cambridge: Harvard University Press.

Wilson, E. O. & Bossert, W. H. (1971). *A Primer of Population Biology.* Sunderland: Sinauer Associates, Inc.

Wright, S. (1931). *Genetics* **16**, 97.

Wright, S. (1945). *Ecology* **26**, 415.

Wright, S. (1949*a*). *Genetics, Paleontology, and Evolution* (G. L. Jepson, *et al.*, Eds). Princeton: Princeton University Press.

Wright, S. (1949*b*). *Proc. Am. Phil. Soc.* **93**, 471.

Wright, S. (1955). *Cold Spring Harbor Symp. Quant. Biol.* **20**, 16.

Wright, S. (1969). *Evolution and the Genetics of Populations: Volume II, The Theory of Gene Frequencies.* Chicago: The University of Chicago Press.

Appendix

Wright's definition of selection, DS-2, must first be explicated. Let:

P = the set consisting of all the alleles in the parental population;

F = the set consisting of all the alleles in the population of the next generation;

A_i = an allele of type i;

A_{ij} = the jth allele of type i.

I am assuming for simplicity that no random effects are present. In addition, each allele has an identifying number. Alleles come in types; assume that all the types of allele present either in P or in F are numbered 1, 2, ... Furthermore, there may be several alleles of a given type within either P or F and these, too, are numbered $A_{i1}, A_{i2} \ldots$

If these sets and their elements (the various alleles) are laid out graphically, imagine drawing a line from each allele in P to each of its daughter alleles in F. If an allele in P has no daughter in F, then that allele will have no line leading from it. On the assumption that each allele in F has only one parent, there is in general a one-many relation between alleles in P and their daughters in F.

Consider an arbitrary element of P, A_{ij}, and its daughter in F. Either the daughter will be of the same type (i) as A_{ij}, or she will not. If she is not, do nothing; if she is, circle her. Do this for each Aij in P, and a three-way partition of F results. Each element in F now has one and only one of the following three properties:

α: It is connected with an element of P, but is not circled.

β: It is connected with an element of P, but is circled.

γ: It is neither connected with an element of P nor is it circled.

Those with α can be interpreted as the unmutated progeny of the alleles in P, while those with β are the mutated progeny of P. Those with γ do not have ancestors in P and are immigrants. Together these alleles constitute the entire F population.

A third set, F^*, is now constructed in the following manner. For each allele in F with α, put that allele in F^* and connect it with a line to the allele in F. For each allele in F with β, put that allele which is its parent in P into F^* and connect it with a line to the allele in F. Do nothing for the γ alleles in F. This completes the construction of F^*.

Finally, the frequency vectors (F^* and P) for F^* and P need to be constructed. The total number of alleles in P is ΣA_{ij} (where the summation is over all i, j), for each A_{ij} in P. There is a corresponding expression for the total number of alleles in F^*. Let $N(P)$ be the total number of alleles in P and $N(F^*)$ be the total number of·alleles in F^*. Then, the frequency of the i allele in P is just $\Sigma A_{ij}/N(P)$, where the summation is over all j. There is a corresponding expression for F^*. Construct the frequency vector, P, for P in the following way. The ith position

in P is the frequency of alleles of type i in P. Also, the ith position in F^* is the frequency of alleles of type i in F^*. Now, what DS-2, Wright's definition of selection, says is that selection occurs if and only if $P \neq F^*$. That is, F^* was constructed to represent the F population after immigration and mutation were neglected. Random effects are assumed to be absent. Thus, according to Wright's definition, selection occurs if and only if $P \neq F^*$.

To show that DS-1 is equivalent to DS-2, construct P, F, F^*, etc. as above; define $S(A_i)$ to be the total number of lines coming out of P from genes of type A_i; define $\Sigma S(A_i)$, where the summation is over i, to be the total number of lines coming out of P; and consider the following.

Assume that $P \neq F^*$, does it follow that there has been non-randomly differential reproduction of alleles in P? Yes, for consider a typical element of F^*, A_{ij}. Either A_{ij} is a perfect replica of an allele in P, or it is not. If A_{ij} is not a perfect replica of an allele in P, then either it is not a perfect replica or it is not a replica at all of an allele in P. But, by the way in which F^* was constructed, every A_{ij} in F^* is a replica of an allele in P and is also a perfect replica. Thus, each A_{ij} is a perfect replica of an allele in P. Moreover, the frequency of A_i alleles in F^* is, by the way F^* was constructed, just equal to $S(A_i)/\Sigma S(A_i)$. Now, if $P \neq F^*$, then $S(A_i)/\Sigma A_{ij}$ (summation over j) will not be equal to $S(A_k)/\Sigma A_{kj}$ (summation over j) for some A_i and A_k, and this is just to say that there has been differential reproduction of distinct genes. Thus, DS-2 implies DS-1.

To show that DS-1 implies DS-2, assume that selection in the DS-1 sense has occurred and consider the following. If differential reproduction has occurred, then for some A_i and A_k, $S(A_i)/\Sigma A_{ij}$ will not equal $S(A_k)/\Sigma A_{kj}$ (summation over j). But if this is true, then obviously P cannot equal F^*. Thus, we may conclude that DS-1 and DS-2 are equivalent.

This demonstration of the equivalence of DS-1 and DS-2 is general. It does not depend upon the genetic organization of the populations or their breeding structures, just as the definitions of selection are independent of these. There are, however, some implicit assumptions to the demonstration. First, in the argument that DS-2 implies DS-1, it was assumed that intragenic recombination resulting in different alleles is a form of mutation. If Wright's definition of mutation as any alteration in the genetic material is accepted, this assumption is unproblematic. Second, emigrants are not counted as part of F (or F^*). This leads to possibly anomalous situations. For example, if 'differential reproduction' is balanced by emigration, it is, assumed for the purpose of DS-1 that no differential reproduction has occurred. In defence of this practice it can be said that evolution is a population phenomenon, that selection is defined for the purpose of understanding evolution, and that emigrants do not contribute to the evolution of a population. A gene which caused its bearers to emigrate would be selected out of a population, unless its decline were otherwise balanced.