The Confusions of Fitness
André Ariew and R. C. Lewontin

ABSTRACT

The central point of this essay is to demonstrate the incommensurability of 'Darwinian fitness' with the numeric values associated with reproductive rates used in population genetics. While sometimes both are called 'fitness', they are distinct concepts coming from distinct explanatory schemes. Further, we try to outline a possible answer to the following question: from the natural properties of organisms and a knowledge of their environment, can we construct an algorithm for a particular kind of organismic life-history pattern that itself will allow us to predict whether a type in the population will increase or decrease relative to other types?

1 Introduction

No concept in evolutionary biology has been more confusing and has produced such a rich philosophical literature as that of fitness. The confusions have arisen because a concept, originally introduced as an inexact metaphor by Darwin, has come to play an analytic role in the formal quantitative dynamics of evolutionary biology. The confusion has arisen from the mistaken belief that a single coherent definition of fitness is required by, and can

be applied over, all dynamics of evolutionary genetics. There is a conviction among philosophers and biologists that somehow a property of fitness must be included in dynamical explanations of evolution through natural selection. Our purpose in this essay is to show that:

(1) The concept of 'fit' as introduced by Darwin in both the *explanandum* and the *explanans* of his theory does not appear in quantitative dynamical theories of genetic change in evolution.

(2) Any attempt to introduce a unitary analogous concept of 'reproductive fitness' into dynamical models as a scalar ordinal, which will explain or predict quantitative changes in the frequency of types, must fail.

(3) This failure is a consequence of the fact that, in different biological situations, different algorithms must be used to connect temporal changes in type frequencies with quantitative information about reproduction, and that in an important fraction of cases, even complete information on relative reproductive rates is insufficient to determine whether a type will increase or decrease relative to others in the population.

(4) Finally, we discuss the central role played by the convention of counting individuals in algorithms that allow prediction of evolutionary changes in population composition.

2 Darwinian fitness

The concept of fitness for Darwin (he did not actually use the term 'fitness', but did refer to individual organisms as being 'fitter', or more or less 'fit' than other individuals) arose from his view of organism and environment. The essence of Darwinism was the rupture between the causes of the properties of individual living beings and the causes of the structure of the world they occupied. The natural properties of individual organisms varied from individual to individual within a species, and the sources of that variation were internal to the ontogeny of the organism. At the same time, the organisms lived in an external world—the environment—whose structure was causally independent of those organisms. Different individual members of a species, then, 'fit' into the environment to different degrees as a consequence of their variant natural properties, and those that made the best 'fit' would survive and reproduce their kind better than those whose 'fit' was poorer. The word 'fit' ('fittest', 'fitness') is a metaphorical extension of its everyday English meaning as the degree to which an object (the organism) matches a pattern that is pre-existent and independently determined (the environment). This metaphorical lock-and-key fitting of the organism into the environment is reflected in the modern concept in ecology of the environmental or ecological 'niche' that species are said to 'occupy'.

In the original Darwinian structure, fitness is a derived property of the natural properties of individuals living in a particular juxtaposition to the structure of the environment. The characteristic Darwinian adaptive explanation is a kind of engineering analysis in which particular natural properties of individual organisms were shown to lead to greater expected reproduction by those individuals in particular environments. This is the project of the so-called 'Ecological geneticists'. There is the implication that the qualitatively diverse natural properties of organisms could be mapped, as a function of the environment, onto a single ordinal variable, so that one organism can be said to be more or less 'fit' than another even when the mediating natural properties are qualitatively different. In this explanatory scheme, the property of fitness plays an ambiguous role, appearing both in the *explanandum* and in the *explanans*. What is to be explained is the origin of the marvelous fit between the natural properties of the individuals that make up a species and the ecological niche that they occupy. The *explanans* is that:

(1) in a previously less fit species, an occasional variant individual arises whose natural properties make it more fit to the environment;

(2) the variant natural properties are heritable;

(3) a consequence of the greater fit is a higher reproductive rate of the variant individual, which, together with (2), results in:

(4) an increase in the representation of the more fit natural properties among individuals of the species in future generations. This 'Darwinian' explanatory structure can be schematized as:

(A) natural properties → fitness to environment → reproductive rates → changes in representation in the population

The classic example of the use of this schema for an observed temporal change is the attempt by Ford and Kettlewell to explain the increase in the melanic form of the moth, *Biston betularia*, since the nineteenth century (*cf*. Ford [1971]). A more recent and more detailed case is the study of changes in body and bill shape over a 30-year period in two of Darwin's Finches, *Geospiza fortis* and *G. scandens* (*cf*. Grant and Grant [2002]).

What is consequential about this Darwinian explanation for the present confusion about fitness is that the dynamic of the *explanans* does not, in fact, depend on fitness, unless the *explanandum* also involves fitness. That is, *if* what is to be explained is the greater (metaphorical) fitness of evolved species, then a connection is required between (metaphorical) fitness of variant individuals and their reproductive properties. But suppose what is to be explained is simply the evolutionary change in the natural properties of species over time, without reference to any claim about their 'fit' to the environment as in schema

(A)? Then all that is needed in the *explanans* is that individuals with variant natural properties appear, that these properties are heritable, and that they are associated with higher reproductive rates, without any recourse to the notion of 'fit' to the environment. This is the explanatory scheme for many genetical models of evolution. To the extent that an engineering story is demanded, it is that there be some mechanical connection between the variant natural properties whose evolution is being followed and the special set of natural properties that constitute reproductive rate. That mechanical connection may be a natural historical one involving the 'fit' to environmental demands, as in schema (A), but it may equally well involve purely internal physiological, morphological and molecular relationships or genetic correlations. Indeed, the 'fit' to the external world of the favored variant may be significantly poorer. For example, as we discuss below, in a species with overlapping generations, if the population is decreasing in numbers, those types that reach reproductive age late will increase in the population. Yet this retarded development may be a consequence of poorer ability to gather the resources necessary for development. Hence, a trait's properties may be less 'fit' to the demands of the environment but increase in the population nevertheless.

The present confusion over the concept of 'fitness' in evolutionary biology has been the consequence of the attempt to find a general attribute, analogous to Darwinian ecological fitness, that will appear in both *explanandum* and *explanans* of evolutionary scenarios independently of any claim about ecology and, indeed, without the requirement of an engineering story at any level. This is the genesis of the concept of 'reproductive fitness' found in modern genetical models of evolution. In the Darwinian theory of natural selection, the natural properties of individuals are the causes of the fitness to the environment, and the fitness to the environment is the cause of reproductive success. In the genetical theory of evolution, the reproductive success of an individual appears as a primary property, and a new kind of formal fitness, 'reproductive fitness', is introduced. This is intended to be a scalar quantity that can be calculated from information on reproduction and which then predicts changes in the representation of types, without the necessity of connecting these reproductive fitnesses to any other natural properties of the organisms. The schema for this explanatory structure is:

(B) natural properties → reproductive rates → 'reproductive fitness' → changes in representation in the population

3 Reproductive fitness and genetical models of evolution

With the rediscovery of the Mendelian principles of inheritance, including the lack of a one-to-one correspondence between genotype and phenotype, and the development of knowledge of the chromosomal basis for the statistical

properties of inheritance patterns during the first quarter of the 20th century, it became apparent that the Darwinian outline of evolution was incomplete, especially in its reliance on a simple resemblance of parent to offspring. The result was the development of current, specifically *genetical*, theories of evolution under natural selection, theories that have essentially no natural historical elements or even internal causal narratives (with the exception of genetic mechanisms) and in which Darwinian 'fit' plays no role. These theoretical structures, developed in R. A. Fisher's 'The Genetical Theory of Natural Selection' ([1930]), J. B. S. Haldane's 'The Causes of Evolution' ([1932]), and S. Wright's 'Evolution in Mendelian Populations' ([1932]), provide the model for modern evolutionary genetics. They have the following common features:

(1) Population composition is characterized by the relative frequencies of various genotypic or phenotypic classes; that is, by the numerosity of different types. This particular form of book-keeping will turn out to be critical to the general problem of fitness.

(2) Reproductive fitnesses (the exact term varies) are assigned to types, not tokens. These fitnesses are the means (statistical expectations) of quantities calculable from the details of reproductive performances of tokens, which vary around the type mean as a consequence of accident, variation in environment, and the segregation of other genes not included in the type definition. The way in which reproductively relevant properties are used to calculate fitnesses also turns out to be critical to the problem of fitness.

(3) 'Evolution' is described as a change in the relative frequency of the classes over time. These changes are a consequence of reproductive fitness differences, of mutations, of migrations. Account may or may not be taken of the realized variation of these factors around their expectations from generation to generation and population to population.

(4) Alternatively, evolution may be described as a change in the population mean reproductive fitness, averaged over all types (for recent discussions on the difference between Darwinian fitness and statistical fitness, see Sober [2001]; Matthen and Ariew [2002]; Walsh, Lewens and Ariew [2002]). The explanation is then of the form:

(C) reproductive rates $\rightarrow$ reproductive fitness $\rightarrow$ change in representation of types.

As we shall see, despite the attempt of these genetical theories of natural selection to create a general abstract structure in which ecological and demographic details are irrelevant, no such structure is possible and no model-independent measure of reproductive fitness can be derived (for a similar view see Rosenberg [in preparation]). Indeed, in most cases the details of the

reproductive performance of a type cannot be mapped onto any scalar variable.

It is important to realize that the motivation for the genetical theory of evolution is the failure of the Darwinian scheme to explain and predict the direction of change of a population solely from the natural properties of organisms and their environments. That failure is a result of the extra considerations required to predict evolution which are the consequence of the mechanisms of inheritance and the details of reproductive schedules. For Darwin, without knowledge of the mechanical details of heredity, it seemed clear that a type that left more offspring in the next generation would increase in representation in the population. But there are two complications. First, the segregation and recombination of genes in sexually-reproducing organisms has the effect that the rate of reproduction *by* a genetic type is not the same as the rate of reproduction *of* a genetic type. Second, for organisms with continuous reproduction and overlapping generations, the age at which a type produces offspring is as consequential for changes in population composition as is the total number of offspring produced by each type. Since these genetic and demographic relationships vary from species to species, different algorithms are required to connect information about reproduction of different types with information about direction of change for populations, as discussed in the next section.

The confusion about fitness is the result of ignoring the fact that a type's Darwinian 'fitness' to the environment implies a single ordinal scalar which will predict the relative increase or decrease of the type, whereas for many kinds of life histories no such predictive scalar quantity can be specified, even though predictions of change can be made from all of the facts about the reproductive schedules. But without such a scalar we cannot state that one type is 'more fit' than another. Had we not ignored this problem, we would not be trying to utilize 'reproductive fitness' (as in schema (C)) as if it were a surrogate for 'Darwinian fitness' (schema (A)). Nor would we think that there is a single unified concept of fitness that fits all dynamical explanations of evolution where natural selection plays a role. Now, we turn to the models for the proof of the failure to specify a scalar quantity that explains or predicts quantitative changes in the frequency of types.

4 The models of reproductive fitness

4.1 The Standard Viability Model

Wright and Haldane, but not Fisher, base their formulations on a simple model of simultaneous reproduction in a sexual population. A population is represented as relative frequencies of alternative genotypes so that absolute

Table 1 Generation t

gametes	A_1		A_2	
frequencies	p_t		$1 - p_t$	
		mating		
zygotes at birth	A_1A_1		A_1A_2	A_2A_2
frequencies	R		H	D
		survivorship		
adults	A_1A_1		A_1A_2	A_2A_2
frequencies	$R' = RV_1/V$		$H' = HV_2/V$	$D' = DV_3/V$

where V_i is the probability of survivorship of type i and V (mean population viability) $= RV_1 + HV_2 + DV_3$.

Table 2 Mendelian segregation

Generation $t + 1$		
gametes	A_1	A_2
frequencies	$p_t + 1 = R' + H'/2$	$1 - p_t + 1 = D' + H'/2$

numbers of individuals do not enter the model. We need consider here only the simplest case, where the alternative genotypes are the different diploid combinations of alternative alleles at some locus, say A_1A_1, A_1A_2 and A_2A_2. These genotypes reproduce completely sexually, and successive generations are discrete with no overlap of individuals. All reproduction can therefore be considered to be simultaneous. The model has the following formal structure shown in Table 1.

A generation begins at the moment of the formation of zygotes from a union of sperm and eggs produced by the previous generation, and the population is characterized by the initial frequencies of the alternative alleles assumed to be the same in the sperm and egg pool. The initial frequencies of the diploid genotypes are a function of the allelic frequencies in the sperm and egg pools and of the rules of mating. The zygotes then develop to sexual maturity when they produce eggs and sperm according to Mendelian rules to form yet another generation and so on. During the period of development from the moment of fertilization to the time of sexual maturity, some individuals survive to reproduce and others do not. The probability of survival of a genotype from egg to adult is its *viability*, and this viability is the 'reproductive fitness' of a genotype. It is assumed that there are no differences in fertility among genotypes and that the viability differences among genotypes are independent both of the relative frequencies of the genotypes and of the absolute number of offspring. Finally, the mean (reproductive) fitness (viability) of the population as a whole is calculated as the average viability of the different genotypic classes weighted by their frequency. The evolution of the population is then followed as the changes from generation to generation in the frequencies of the alternative alleles at the locus in the sperm and

egg pools, or as the frequencies of genotypes at the same moment in the reproductive cycle in successive generations, or as change in the mean population fitness from generation to generation.

This Standard Viability Model predicts rates of change of the frequency of allelic types across generations, and shows that if heterozygotes are more viable than homozygotes an intermediate stable equilibrium of frequency will be reached. Most powerful in its apparent implications is the analytic result that the average fitness (viability) of the population as a whole increases during the evolution (Fisher) and reaches a maximum when the selective process comes to a final end (Wright), either because the population consists of a single most-fit genotype, or because it is at the intermediate stable equilibrium of frequencies predicted from the viabilities in the case that heterozygotes are more viable than homozygotes. This principle of the maximization of mean reproductive fitness has done an immense amount of work in evolutionary theory, especially because of its analogy with Darwinian notions of ecological fitness.

4.2 Frequency-dependent selection

The assumption in the Standard Viability Model that fitnesses are independent of the frequencies of the genotypes is generally incorrect. It is quite common that rarer types are at an advantage, as in the famous cases of butterfly mimicry where the advantage of having a pattern resembling a species that is distasteful to predators decreases as the palatable mimic increases in numbers. Fitness in frequency-dependent models is not a scalar but a set of functions of genotypic frequency, so that it is not possible to order the fitnesses of the genotypes except at a given frequency. It may be objected that genotypic frequencies are simply an environmental variable and that it has never been claimed that fitnesses are independent of environment, so no added ambiguity is introduced by the frequency-dependent case. An additional problem is that in the frequency-dependent case, the induced change in fitnesses consequent on changes in genotypic frequency may lead to a decrease rather than an increase in mean population fitness, and no optimal fitness principle applies (Lewontin [1958]).

4.3 Fertility models

When it is allowed that there are fertility as well as viability differences among genotypes, the problem of assignment of fitnesses to genotypes becomes even greater. In general, a mating pair determines fertility so that, in the simplest case of a population with two allelic variants at a locus, there are nine mating pair types and the net fertility of a given genotype is a function of the relative

frequencies with which these mating pair types form. Again it may be claimed that the fitness of a genotype is simply contingent on its mate as it is on other environmental circumstances, and that one can calculate the net (mean) fertility of each genotype for the particular distribution of potential mates. The problem, however, is that the genotypic identities of the offspring of an individual of a given genotype also depend upon the genotype of its mate, so these net (mean) fertilities are insufficient to generate the frequencies of offspring in the next generation.

A second difficulty in the definition of fitnesses when there are fertility differences arises when variations in absolute numbers of offspring are considered, even in the simplest case of asexual reproduction. An example is given by Sober ([2001]). Suppose Type A always produces two offspring while Type B produces one individual in some generations and three individuals in others, with equal probability. Thus the expectation of the reproductive rate of the two types is equal (two). Suppose we begin with two individuals of each type. In the next generation there will be four Type As and either two or six Type Bs with equal probability. Then the expected relative frequency of the two types in the next generation is:

$$\text{Type A} = (.5)(4/6 + 4/10) = .535$$
$$\text{Type B} = (.5)(2/6 + 6/10) = .465$$

This discrepancy between the equality of expected reproductive rates and the inequality of expected relative frequency in the next generation arises from the difference between the expectation of a ratio and the ratio of expectations. The type with the lower variation in reproductive rate has the greater long-term expectation. Which, then, is the correct measure of fitness?

4.4 Overlapping generations

A major fraction of living species, like humans, do not have discrete, non-overlapping generations. Each mating pair produces offspring over an extended period and these in turn reproduce over many ages. As a consequence, the time rate of change of a particular genotype in a population depends not only on the total number of offspring of the genotype, but also on the ages at which those offspring are produced, since it depends on the number of successive offspring generations that are produced per unit time. Thus the relevant reproductive information for a genotype is the complete age-specific survivorship and fertility schedule of the type. What is the probability that an individual will reach age x and, given that it reaches that age, what is the expected number of births it will produce between age x and $x + dx$? The problem is to map the age-specific survivorship and fertility schedule onto

a scalar, fitness. Fisher ([1930]) built his entire structure of evolutionary genetics on the model of overlapping generations using an erroneous method of converting age-specific survivorship and fertility into reproductive fitness. He reasoned as follows: it is a basic result of demographic theory that a population characterized by a particular age-schedule of survivorship and fertility will eventually reach a stable distribution of ages, the stable age pyramid. When it does so, the total population size will then grow at a steady geometric rate m, given by the solution to the Euler equation:

$$\int e^{-mx} l_x b_x \, dx = 1$$

where l_x is the probability of surviving to age x, and b_x is the expected number of births to an individual aged x. He called m the Malthusian parameter. If a population consists of a mixture of genotypes, each with a different l_x and b_x schedule, then the Malthusian parameter for each should predict the rate of increase of that genotype in the population relative to the other genotypes. The error in this argument is that it leaves out sexual reproduction and Mendelism. It confuses the rate of reproduction *by* a genotype with the rate of reproduction *of* a genotype. Mendelian segregation and reassortment has the effect that heterozygotes produce both homozygotes and heterozygotes, while a homozygote A_1A_1 will produce heterozygotes if it mates with a homozygote A_2A_2. Thus, genotypes do not increase or decrease in a population as if they were each separate species with characteristic age-specific reproductive rates. In fact, there is no mapping possible of these age-specific rates onto scalar quantities associated with genotypes that can be used to predict changes in genetic composition of a sexual population. The minimum dynamic model for predicting genetic changes requires the complete specification of the age-specific rates as calculating devices (Charlesworth and Giesel [1972]). Indeed, even the complete relative age-specific rate schedules are not sufficient. It is also necessary to know whether the population as a whole is increasing or decreasing in size, which requires both the absolute age-specific mortality and fertility schedules and the age distribution of individuals in the population. Charlesworth and Giesel ([*Ibid.*]) give an example of two genotypes with different reproductive schedules that differ in the timing of reproduction, such that the first produces its offspring at an early age, while the second delays reproduction to a later age. This is an example of the demonstration by Demetrius ([1992]) of the dependence of genotype dynamics on the demography and growth rate of the population. If the population as a whole is increasing in size, the first, precocious, genotype increases in frequency, while if the population size is decreasing, it is the second genotype that increases relative to the first.

   We are forced to conclude that for species with overlapping generations, i.e. for a very large fraction of organisms, no scalar reproductive fitness measure

can be derived from reproductive schedules that allows statements of the form 'Type A is more fit than type B.'

5 Fitness as outcome

The recognition of difficulties in deriving a general measure of reproductive fitness from reproductive properties has led some evolutionary theorists and philosophers to propose that reproductive fitness should be measured from the trajectory of change in type abundances rather than as a scalar calculable from reproductive information that would predict such change (see, for example Price [1995]; Michod [1999]; Rosenberg [1983]). Our criticism of this move follows the lines already laid down by others (see Krimbas [2002] for a detailed analysis). First, it is unclear what work is done by a measurement of fitness as effect. Since it identifies fitness differences with changes in frequency of types, it has no power to explain those changes. Second, beyond a general extrapolatory use, that changes in type frequency which have been observed will continue in the future, it has only the weakest predictive power. It could not predict, for example, prospective intermediate equilibrium of type frequencies. Third, as we illustrate below, it may lead to incorrect conclusions, if fitness so defined is taken to be an indicator of the causes of type frequency histories.

5.1 Fitness as actual increase in type

The problem with using observed frequency changes is that no distinction can be made among different explanations of these changes, in particular between different natural properties of individuals that are relevant to their expected reproduction and factors that are orthogonal to those properties, so-called 'random events'. Chief among these in a finite population of organisms, each producing a small number of offspring, is the random sampling of the gamete pool at each mating. If two types are in equal frequency in some initial generation, they will become unequal in frequency and, if enough generations elapse, one will disappear by this random drift process even in the absence of expected differences in reproductive behavior. To associate the quality of 'superior fitness' to the one that survives while claiming that nothing causal is implied is perverse, given the usual use of the notion of 'fitness'. Either no explanatory work is done, or an explanation is incorrectly implied.

5.2 Fitness as expected increase in type

5.2.1 Expected increase within a generation

Price ([1995]) defines the fitness of the ith type as

$$W_i = f'_i/f_i$$

where f′ and f are the expected frequencies of the type before and after selection within a generation. But such a definition is derived from the standard discrete generation viability model. Suppose, for example, that the genotypes A_1A_1 and A_2A_2 are unable to reach adulthood, but that the heterozygote is perfectly viable. The population reaches an equilibrium with genotypic frequencies .25, .5 and .25 at conception, but at adulthood the homozygotes are completely absent, so their fitnesses are estimated, reasonably, as 0. But suppose, in contrast, that the homozygotes are perfectly viable but completely sterile while the heterozygote A_1A_2 is fertile. At equilibrium, the three genotypes will be in frequencies .25, .5 and .25 throughout the generation and offspring will be produced all during the generation in those same proportions as a consequence of Mendelian segregation, so it must be judged that there are no reproductive fitness differences, despite the large differences in fertility.

Fisher ([1928]), on the other hand, defined the relative fitness as the Malthusian parameter, m, but as we have seen, this erroneous use of the Euler formula results in fitness values that have no determined relation to changes in population composition.

5.2.2 Expected increase between generations

This definition confounds the absence of selective differences between types with a stable equilibrium of types expected under some schemes of selection. The cases of the sterile and inviable homozygotes given in the previous section are examples. In no case where there is an equilibrium will fitness differences appear when between-generation changes in type frequencies are used. It might be claimed that if no changes in type frequencies are occurring then, indeed, there are no net fitness differences at equilibrium, and that the equilibrium is a consequence of reproductive differences balancing out. But this confounds differential reproduction with the effect of Mendelian segregation and reassortment. There is no balance of reproductive differences at equilibrium. In the example of the inviable homozygotes, genotypes are being removed from the population within a generation by differential death, and they are being exactly replaced at the beginning of the next generation by Mendelian segregation and reassortment from the heterozygotes. The balance is not between fitnesses, but between survivorship differences on the one hand and the Mendelian mechanism on the other. This can easily be seen by imagining what would happen if sexual recombination were turned off in this case and the genotypes reproduced entirely by vegetative means. In a single generation all homozygotes would disappear permanently and the population would consist of nothing but heterozygotes. The use of expected changes between generations to define fitness confounds variation in the

natural properties of organisms that lead to differential reproduction with the consequences of a mechanism of inheritance that is common to all the organisms.

5.2.3 Postponed reproductive fitness effects

There are a number of cases in which the effect of a genotype is neither on the viability nor the fertility of the immediate carrier of the genotype, but of its offspring. For example, if a bird were deficient in the provisioning of its nestlings, those malnourished offspring might have reduced fertility when they, in turn, became reproductive adults. The classic example of a postponed reproductive fitness effect is the recessive *grandchildless* (*gs*) mutation in *Drosophila subobscura*. Females homozygous for the mutation (*gs/gs*) have normal viability and fertility. However, the eggs they produce have an abnormal internal structure which has the effect that the adults that develop from these eggs cannot themselves produce sperm or eggs, irrespective of their own genotype. Thus the *gs/gs* homozygous females have normal numbers of offspring which may be *gs/gs* or *gs/+*, but no 'grandchildren' of any genotype. The attempt to characterize the reproductive fitness of *gs/gs* females by the ratio of the frequency of this genotype at birth to the frequency among adults within a generation will obviously miss the fertility effect. Using the ratio of genotypes between equivalent stages of two successive generations will certainly detect some change, but will appear as a deficiency in both *gs/gs* and *gs/+* genotypes, even though it is only the former that is the source of the reproductive fitness difference. Moreover the comparison of the apparent reproductive fitness differences over a series of generations will show the fitness difference to be frequency dependent, whereas it is, in fact, an unconditional defect of the *gs/gs* type.

6 The book-keeping problem

The purpose of assigning reproductive fitnesses to types is to make possible some prediction or retrospective explanation of the change in representation of those types over time. But to predict increases or decreases in representation we need to begin with some decision about the variable in which representation is to be measured. The traditional method has been to count individuals of different types, but this apparently unproblematic individuation does not always work. For example, violets reproduce in two ways. A flower may set seed and these seeds, having dispersed, may each give rise to a new plant. Alternatively, a violet stem may send out underground runners which, at points along their lengths, put up flowering stalks. A plant produced from seed is *genet* while one produced above ground asexually from a runner is a

ramet. The problem that has plagued evolutionists who deal with organisms that have both sexual and vegetative reproduction is how to count ramets and genets in assigning reproductive fitness. Do all the ramets of a single original stem count as belonging to a single individual, or is each to be counted as a separate individual? It might be argued that since the ramets are all connected as a single body, they are collectively one individual. But is the occurrence of a break in the underground stem sufficient to produce a new individual for accounting purposes? Moreover, the problem exists for trees. A tree consists of a large number of flowering stems connected together by branches and a trunk. Why should it matter that these flowering stems are connected above ground rather than below? If a tree is a single individual then so is the collection of all the ramets of a violet. How is fitness to be calculated in such instances? Suppose an entire field is occupied by hundreds of ramets from a single original plant, except that in one spot there is a single plant that is a genet of a different type. Are the two types to be counted as equally frequent? In a colonial organism, say a coral, is a type that produces a single colony that spreads to occupy nearly the entire territory available to a species less evolutionarily successful than a type that reproduces 100 scattered sexually-reproduced organisms, each of small extent? It would appear that the problem of fitness and relative evolutionary success demands a solution to the problem of defining an individual.

The problem raised by individuation is a consequence of the Malthusian origin of evolutionary theory. The book-keeping of evolutionary biology in terms of numerosity is the transfer onto the evolutionary problematic (and onto a great deal of ecological theory as well) of the central problem of human demography, the growth in numbers that arises from using as a model a sexual species that reproduces solely by giving birth to clearly defined individual objects that all grow to approximately the same size.

As an alternative it would be possible to build a dynamical theory that used not numbers of denumerable objects, but a continuous measure of occupancy of the external world, for example the total amount of living protoplasm belonging to a given type. Indeed the Malthusian preoccupation with numbers stemmed from a preoccupation with the supposed limit in the resources available and the struggle to acquire those resources that were in limited supply. But success in sequestering resources in short supply is measured by the total amount sequestered. In the special case that there are well-defined individuals of approximately the same size, numerosity is a proxy for total resource, but it is only a proxy. (It should be noted that, in present-day political analyses of human ecology, a great deal of attention is paid to the fact that some people use a great deal more resources and

produce a great deal more pollutants than others.) The question, then, is what continuous measure should be used for a dynamical theory. There were some attempts to build a theoretical population ecology on the basis of energy fluxes (see, for example, Margaleff [1968]), and population geneticists have occasionally used biomass as a measure of population fitness (Dobzhansky and Pavlovsky [1961]), but the relation between biomass or energy flux and a dynamical genetical theory of natural selection is not clear. *A priori*, the most direct connection between evolutionary change and a continuous measure of fitness would be to use the proportion of the limiting resources for species reproduction that is pre-empted by a given type. Evolutionary change would then be measured as the change in the total proportion of the limiting resource occupied by the various types. Again, in the case of unproblematic individuation of objects of roughly equal resource occupancy, simple numerosity would be an adequate proxy.

The difficulty of replacing numerosity by limiting-resource occupancy is that dynamic evolutionary models could no longer be usefully framed in generalized abstract terms. Frequency-dependent selection is usually ignored because predictions depend on the exact form of the frequency dependence, and although there are classes of mathematical functions that can be treated as essentially alike, it is necessary in each application to determine to which of these function classes, if any, the problem belongs. The use of a limiting-resource theory is even more difficult because it demands detailed natural historical and physiological information in each case.

7 Conclusion

It appears that the resolution of the confusions about fitness requires three clarifications. First, we must not conflate the genetical notion of 'reproductive fitness' with the Darwinian metaphor of organisms 'fitting' more or less into an environmental niche. Second, we require the abandonment of the attempt to make a general quantitative dynamical theory of evolutionary change in which a unitary scalar, 'reproductive fitness', appears as a parameter, and the acceptance of a diversity of specific dynamical models in which variation in reproduction among heritable types appears in structurally quite specific ways. Finally, if reproductive fitness differences are to predict or explain changes in representation of types in evolution, it requires, in each case, a decision about the nature of the scale on which the representation of different types is to be measured.

Acknowledgements

André Ariew   *R. C. Lewontin*
Department of Philosophy   *Museum of Comparative Zoology*
University of Rhode Island   *Harvard University*
Kingston, RI 02881   *Cambridge, MA 02138*
U.S.A   *U.S.A*
ariew@uri.edu   *lewontin@oeb.harvard.edu*

References

Charlesworth, B. and Giesel, J. T. [1972]: 'Selection in Populations with Overlapping Generations. II: Relations Between Gene Frequency Change and Demographic Variables', *American Naturalist*, **106**, pp. 388–401.

Demetrius, L. [1992]: 'Growth Rate, Population Entropy and Evolutionary Dynamics', *Theoretical Population Biology*, **41**, pp. 208–36.

Dobzhansky, T. and Pavlovsky, O. [1961]: 'A Further Study of Fitness of Chromosomally Polymorphic and Monomorphic Populations of *Drosophila pseudoobscura*', *Heredity*, **16**, pp. 169–77.

Fisher, R. A. [1930]: *The Genetical Theory of Natural Selection*, Oxford: Oxford University Press.

Ford, E. B. [1971]: *Ecological Genetics*, 3rd edn, London: Chapman and Hall.

Grant, P. R. and Grant, B. R. [2002]: 'Unpredictable Evolution in a 30-year Study of Darwin's Finches', *Science*, **296**, pp. 707–11.

Haldane, J. B. S. [1932]: *The Causes of Evolution*, London: Harper and Bros.

Krimbas, C. B. [2001]: 'Fitness', *Encyclopedia of Genetics*, Academic Press, **2**, pp. 702–6.

Lewontin, R. C. [1958]: 'A General Method for Investigating the Equilibrium of Gene Frequencies in a Population', *Genetics*, **43**, pp. 419–34.

Margalef, R. [1968]: *Perspectives in Evolutionary Theory*, Chicago, IL: University of Chicago Press.

Mathen, M. and Ariew, A. [2002]: 'Two Ways of Thinking About Fitness and Natural Selection', *Journal of Philosophy*, **99:2**, pp. 55–83.

Michod, R. E. [1999]: *Darwinian Dynamics*, Princeton, NJ: Princeton University Press.

Price, G. R. [1955]: 'The Nature of Selection', *Journal of Theoretical Biology*, **175**, pp. 389–96.

Rosenberg, A. [1983]: 'Fitness', *The Journal of Philosophy*, **80**, pp. 457–73.

Rosenberg, A. [MS]: 'Fitness, Probability and the Principles of Natural Selection'; in preparation.

Sober, E. [2001]: 'The Two Faces of Fitness', in Singh, et al. (*eds*), 2001, *Thinking About Evolution*, Cambridge: Cambridge University Press.

Walsh, D., Lewens, T. and Ariew, A. [2002]: 'The Trials of Life: Natural Selection and Random Drift', *Philosophy of Science*, **69**, pp. 429–46.

Wright, S. [1931]: 'Evolution in Mendelian Populations', *Genetics*, **16**, pp. 97–159.