Fitness

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Fitness is a measure of the survival and reproductive success of an entity. This entity may be a gene, individual, group or population.

Fitness as Survival and Fertility

Can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, would have the best chance of surviving and of procreating their kind. On the other hand, we may feel sure that any variation in the least degree injurious would be rigidly destroyed. This preservation of favourable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or Survival of the Fittest (Darwin, 1859).

All current uses of the term 'fitness' in evolutionary biology are related to the theory of natural selection. Darwin used the term 'fittest' to describe those individuals that are best able to survive (most viable) and reproduce (most fertile). Because organisms with different traits have different abilities to survive and reproduce (and consequently different fitnesses) and because there is a tendency for offspring to resemble their parents, the composition of a population will change over time. Understanding fitness and its components is therefore key to an understanding of evolutionary change.

Although it was clear in Darwin's time that some form of inheritance existed, the physical structure and properties of the inherited material were unknown. We now know that every organism, with the exception of certain RNA viruses, inherits from its parents a genetic blueprint encoded in one or more molecules of DNA. An organism develops according to the complex interaction of its genetic code and the environment to produce individual organisms with different phenotypes. As recognized by Darwin, some of these phenotypes provide their bearers with enhanced viability and fertility. As a result, alleles that give rise to such phenotypes tend to make up a greater proportion of the population in successive generations. Because alleles from different individuals are continually mixed through sexual reproduction, evolutionary biologists are primarily interested in the fitness or reproductive success of alleles or genes. To this end, the fitness of an allele is usually defined as its contribution, through its effect on the viability and fertility of its bearers, to the future gene pool. Here we have left unspecified the time frame over which fitness is measured since this depends on the type of organism and question under consideration. For example, Darwinian fitness (W) is measured over one organismal generation, while Malthusian fitness (m) is a measure of fitness over a very small period of time ('instantaneous').

The fitness of an allele as measured by its contribution to the future gene pool will necessarily depend on the time scale over which it is measured. For some questions, the appropriate time scale may be longer than one generation. For example, consider Fisher's explanation for why many populations exhibit a 50:50 sex ratio (Fisher, 1930). He pointed out that, if the sex ratio is not 50:50, then any allele that causes its bearer to overproduce the rare sex will make a larger contribution to the future gene pool. Notice that the mutant allele does not alter its bearer's fertility or viability, but simply causes most of its offspring to be of the sex in short supply. As a result, these offspring obtain a greater number of matings, on average. Therefore, the allele's increased contribution to the future gene pool (i.e. its increased fitness) is realized two generations into the future (**Figure 1**).

One can define fitness for entities at other levels of the biological hierarchy besides alleles, including individuals, groups of individuals, and even populations or species. Often, the fitness effects of an allele must be considered at several of these levels to determine the allele's overall fitness. For example, in most diploid sexual organisms, Mendelian segregation during meiosis ensures that each chromosome of a homologous pair has a 50% chance of being passed to an offspring. There are exceptions, however, to Mendelian segregation where certain chromosomes are transmitted more frequently to offspring, a phenomenon known as meiotic drive or segregation distortion. An example is the tailless allele (t) in mice, which is passed to roughly 95% of the offspring of heterozygous, $T\,t$, males (Lewontin and Dunn, 1960). Yet individuals that are homozygous for the t allele often die before birth or, if they survive and are male, are sterile. Therefore, to understand the evolutionary fate of the t allele, it is necessary to consider its fitness at two levels, within individuals and between individuals. The t allele has a higher fitness within an individual because of its higher transmission to offspring (higher fertility), but it has a lower fitness at the 'between individual' level. To determine the expected contribution of the t allele to future generations requires that both of these opposing fitness effects be considered.
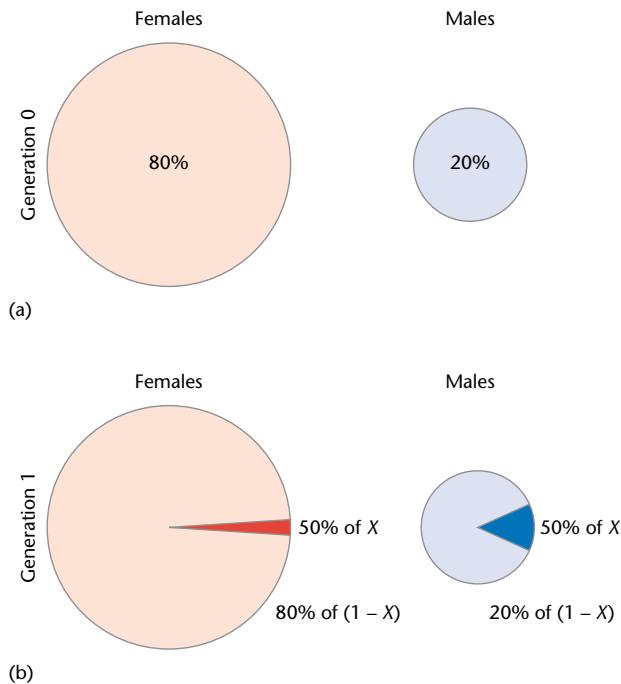
Females

(a)

Males

(b)

Figure 1 Fitness and the sex ratio. Mothers that produce an equal number of sons and daughters will have a higher long-term fitness than mothers that produce an unequal sex ratio, even if all individuals have the same survival and fertility.

(a) For example, imagine a population that initially contains 80% females and 20% males. (b) Now consider a new type of mother that produces 50% daughters and 50% sons. If this new type represents X% of the mothers, their children will account for X% of the population in the next generation, but they will account for a much larger proportion of the males.

Because each offspring in generation 2 must have exactly one mother and one father, the new type of mother from generation 0 will have more grandchildren, on average, because her sons will make up a disproportionately large fraction of the rarer sex (males).

Absolute Versus Relative Fitness

The definition of allelic fitness given above also leaves the word 'contribution' unspecified. If this contribution is measured as the allele's expected number of offspring (i.e. number of copies) at some specified point in the future, then this is termed its absolute fitness. Similarly, the absolute fitness of an individual (or a genotype) is simply its expected number of surviving offspring. The absolute fitness of an individual determines how many individuals there will be in the following generations.

Since alleles tend to increase or decrease in frequency relative to the frequency of other alleles, knowledge of relative fitness (**Table 1**) is often sufficient to predict evolutionary change. That is, the absolute number of offspring per parent need not be known, only the extent to which each type over- or under-reproduces when compared to some reference. This is fortunate, since often it is easier to measure relative than absolute fitness (see below).

For example, consider a single locus at which there are two alleles, A and a, under natural selection. A diploid population consists of three types of individuals: AA, Aa and aa. Let us denote the absolute fitness of each of these types by $W(AA)$, $W(Aa)$, and $W(aa)$, respectively. Relative fitnesses can be obtained in any number of ways. For example, one can divide the absolute fitness of each type by the average absolute fitness of all types. Alternatively, one can choose a reference genotype and divide the absolute fitness of each genotype by the absolute fitness of the reference type (**Table 1**). Relative fitnesses are often written as 1 for AA, $1 + hs$ for Aa, and $1 + s$ for aa individuals, where s and h are known as selection and dominance coefficients, respectively. The selection coefficient measures the strength of selection favouring the a allele. If s is positive then aa individuals have a greater relative fitness than AA individuals and vice versa. The

Table 1 Relationships between absolute fitness, relative fitness and selection coefficients[a]

	Genotype		
	AA	Aa	aa
Absolute fitness	$W(AA)$	$W(Aa)$	$A(aa)$
Relative fitness	$\dfrac{W(AA)}{W(AA)} = 1$	$\dfrac{W(Aa)}{W(AA)} = 1 + hs$	$\dfrac{W(aa)}{W(AA)} = 1 + s$
Example			
Absolute fitness	1.40	1.75	2.10
Relative fitness	1.00	1.25	1.50
Selection coefficients	$s = 0.5$		$h = 0.5$

[a]In the table, relative fitness is measured against the fitness of AA individuals. Although the notation used in the table is standard, alternative definitions are often encountered. For example, the fitness cost of a deleterious allele is often defined as s, such that the fitness of an individual is $1 - s$. The notation is arbitrary as long as one can determine the relative fitness of each type. The selection coefficient here is given by s and the dominance coefficient is given by h.

dominance coefficient measures the extent to which the fitness of *Aa* heterozygotes resembles the fitness of *aa* (high *h*) or *AA* (low *h*) individuals.

Knowledge of either absolute fitnesses, relative fitnesses or selection coefficients can be used in many mathematical models to predict the rate of change of an allele. In the simplest case, when the relative fitnesses are 1, $1 + s/2$, and $1 + s$ (additive allelic effects; $h = 1/2$), the frequency of allele *a* (call this *p*) changes over a generation by an amount:

$$\Delta p = sp(1 - p)/2 \qquad [1]$$

(Crow and Kimura, 1970). This illustrates the point that rates of evolutionary change are directly related to measures of fitness.

Estimating Fitness Empirically

One direct way to estimate the relative fitness of an allele is to measure the change in its frequency through time. This is a definitive measure of its contribution to future generations, but a potential difficulty with this approach is that allele frequencies can change for reasons unrelated to fitness (e.g. immigration from areas with different allele frequencies).

Another approach is to estimate the Darwinian fitness of individuals of known genotypes. Estimates of the fitness of individuals can then be used to determine the average fitness of an allele within the population. This approach is labour-intensive, since many individuals must be tracked to obtain good estimates of survival and fertility. Rarely is this approach used for more than a single generation. Because of the difficulties of estimating the fitness of individuals, another approach is to measure a surrogate of individual fitness. For example, in many organisms it may be reasonable to assume that an individual's reproductive success is related to its ability to acquire resources. Consequently, some scientists have used energy gain or growth rate by individuals as a surrogate measure of fitness. Alternatively, researchers sometimes focus on a single component of fitness (e.g. survival or fertility) and make the assumption that other components will behave similarly. For example, a researcher might mark all the young individuals in a population, and return at a later time to determine which types of individuals were best able to survive over this time period. In other organisms, birds for example, it might be easier to estimate fertility than survival by counting the number of eggs in a nest. Measuring only a component of fitness is risky, however, since trade-offs often exist among different components. For example, producing a large clutch of eggs might reduce a mother's chance of surviving the winter. Measuring one aspect alone would give inaccurate fitness measures and incorrect predictions of evolutionary change.

For organisms with short generation times, such as bacteria, researchers tend instead to measure the instantaneous rate of change of each type, i.e. Malthusian fitness, *m*. For example, if an initial population consists of N_0 individuals and grows to N_t individuals in an amount of time *t*, then *m* can be estimated from:

$$m = \ln(N_t/N_0)/t \qquad [2]$$

In simple cases, the Malthusian fitness parameter can also be related to rates of evolutionary change within a population (Crow and Kimura, 1970).

Fitness is Environment Dependent

It cannot be overemphasized that fitness depends on the environment, including both the physical (abiotic) and biological (biotic) environment. An allele's absolute fitness often changes if abiotic factors such as moisture or temperature change. Even the relative fitnesses of alleles may change; for example, relative fitnesses often show greater differences under harsh conditions. Equally important, an allele's fitness often changes when its biotic environment changes. This includes changes in the populations of other species that are present and changes in the size and composition of its own population. These considerations reveal that fitness will often change through time, which has extremely important implications. In particular, the allele that currently has the highest fitness may not have the highest fitness at other times and may never become common within the population.

To illustrate this point, consider a population of asexually reproducing organisms in which there are two alleles (*A* and *B*) that code for different types of individuals. Furthermore, suppose that the absolute fitness of these two types (i.e. the average number of descendants in the next generation) depends on whether the environment is wet or dry (**Figure 2**). How will the population evolve if the environment alternates between wet and dry over time? The table of **Figure 2** shows that *B* is favoured (i.e. it has a higher fitness) in dry years, and *A* is favoured (i.e. it has a higher fitness) in wet years. Therefore, knowing the average fitness of the two alleles in a given environment does not allow a prediction of the long-term outcome of evolution. Surprisingly, knowing the average fitness of the two alleles across the two environments does not allow a prediction of the long-term outcome either. In particular, the average fitness of both alleles in **Figure 2** is the same (5/4), yet allele B eventually comes to dominate the population (**Figure 2**). In this case, it is the geometric mean fitness that accurately predicts the long-term outcome of evolution (Haldane and Jayakar, 1963).
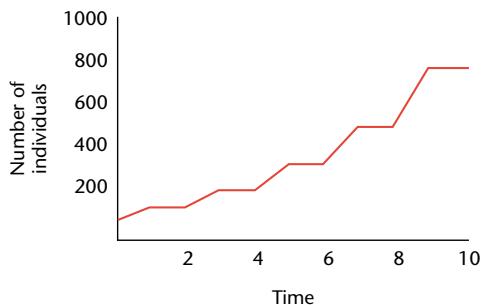
In many cases, the number of individuals of the same species that are competing for resources can have a large impact on fitness. In such cases, fitness is said to be density

(a)
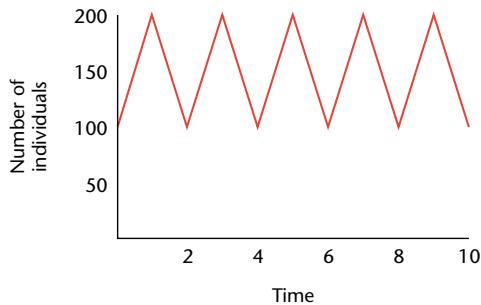
(b)

(c)

Figure 2 Geometric mean fitness. If the fitness of a type varies over time, its geometric mean fitness determines whether it will spread or disappear (Haldane and Jayakar, 1963).

(a) For example, consider two environments (wet and dry) that alternate from generation to generation, and two types of individuals (A, B), whose absolute fitness depends on the environment. (b) Starting with 100 A individuals in a wet environment, there will be $100 \times 2 = 200$ offspring produced. The environment then becomes dry, and these 200 individuals produce $200 \times 1/2 = 100$ offspring. This creates a seesaw pattern over time. (c) Starting with 100 B individuals, however, $100 \times 3/2 = 150$ offspring are produced in the first generation (in the wet environment). These produce $150 \times 1 = 150$ offspring in the next generation (in the dry environment). The cycle begins again, but now with more individuals.

In this example, types A and B have the same average fitness (5/4) over the two environments but different geometric mean fitnesses. Since the geometric mean of fitnesses, W_i, measured over T generations equals $(W_1 W_2 ... W_T)^{1/T}$, the geometric mean fitness of type B is higher (1.2) than that of type A (1.0) and accurately predicts the spread of B.

dependent. To understand evolution under such circumstances, it is important to consider absolute fitness, in addition to relative fitness, because it is the absolute fitness of individuals that determines population size. In other words, fitness differences among individuals can have both ecological and evolutionary implications, and these cannot be considered in isolation of one another.

Frequency-dependent fitness

When an allele's fitness depends on the frequency of other alleles at the same locus, fitness is said to be frequency dependent. At the individual level, fitness is frequency dependent if an individual's fitness depends on the frequency of the types of individuals in the population. The example of sex ratio evolution mentioned above is one such case, where the fitness of an individual depends on the frequency of each sex within the population. Another type of frequency dependence occurs when there are genetic interactions among loci ('epistasis'). In this case, the relative fitness of an allele will depend on which alleles are present at other loci, and therefore its fitness will change as the genetic composition of the population changes at these other loci.

Frequency-dependent fitness is a special type of environment-dependent fitness; it too can cause fitnesses to change through time. Importantly, it is evolutionary change itself (that is, changes in the frequencies of different alleles) that causes the fitness of each allele to change over time. This feedback between evolutionary change and fitness can have important and unexpected consequences. For example, it is possible that a rare allele that currently has the highest fitness and makes the greatest contribution to the next generation actually makes the smallest contribution to subsequent generations once it becomes common. This is an important mechanism through which polymorphism can be maintained.

Derived Measures of Fitness

In the simplest cases, where individuals do not interact and have constant fitnesses, fairly simple predictions can be made about how allele frequencies change over time based on these fitnesses (as in eqn [1]). Real world organisms do interact, however, and have fitnesses that change over time. In such cases, fitness in any particular generation may not have predictive value in the long term. Consequently, to predict the outcome of evolution, biologists have tried to derive other measures of fitness that are maximized by natural selection for many scenarios of interest. A few examples will illustrate the utility of this approach.

Because fitness usually changes when the environment changes, it is often very difficult to predict evolutionary outcomes. For instance, in the above example of a

temporally fluctuating environment, with wet years and dry years, it is not a simple matter to determine which allele will come to dominate in the long run. To do so requires that one carefully keep track of how allele frequencies change each generation. Such bookkeeping reveals that it is the allele with the greatest geometric mean fitness that eventually dominates the population in a temporally varying environment. Consequently, it is convenient to think of the geometric mean fitness as 'the appropriate measure of fitness' in this context.

Consider another example. In many social organisms, some individuals forgo reproduction and help other individuals raise their offspring. At first glance, such altruism is difficult to explain because helpers appear to have zero fitness. The first clear explanation for this phenomenon was given by William Hamilton (1964). The key, he found, was to consider altruism from the perspective of an allele residing in a helper. If the individual receiving help also contains a copy of this allele, then altruism can sometimes enhance the allele's contribution to the next generation. Hamilton demonstrated this by carefully keeping track of how the allele frequencies change from one generation to the next when such interactions occur. Hamilton's most important insight, however, was that this complicated bookkeeping could be reduced to a much simpler system by defining a new measure of fitness. First, he supposed that the helping behaviour of the altruist reduces its fitness by an amount $-c$, and that the individual receiving the help has its fitness increased by an amount b. From these, the 'inclusive fitness effect' of the altruistic behaviour is defined as the sum of its effect on the fitness of the altruist and its effects on the fitness of the beneficiary, with the latter effect weighted by the genetic relatedness of the beneficiary to the altruist, r. In other words, the inclusive fitness effect of the altruistic behaviour is $-c + br$. Hamilton then showed that an allele at a locus that causes its bearers to act altruistically can spread whenever this inclusive fitness effect is positive: $br > c$. This condition is known as 'Hamilton's rule' for the spread of altruism.

Alternative measures of fitness have been defined for other contexts as well. An important example is when a population consists of individuals of different ages (x), each of which may have different degrees of reproductive success (m_x) and different chances of having survived from birth (l_x). Evolution within age-structured populations was extensively studied by Charlesworth (1980). He was able to show that, under certain special circumstances, the intrinsic growth rates of the alleles (which are essentially their Malthusian fitnesses) determine the rate and direction of evolutionary change. The intrinsic growth rate of an allele, which can be calculated from the m_x and l_x for each age class, is therefore a more appropriate measure of fitness than say the average number of offspring per parent, which does not predict whether or not an allele will spread.

In all instances where alternative fitness functions have been defined, they are simply tools for predicting the outcome of evolution through natural selection. These alternative functions can be applied to predict the outcome of evolutionary change simply by plugging in data on fitness into the appropriate fitness function and determining which type has the highest fitness. The simplicity of this approach is attractive, but it has its pitfalls. Most importantly, the mathematical derivations depend on certain assumptions, which are easily overlooked. For example, the above fitness measures adequately predict allele frequency change only when genetic associations with other loci and density effects are small. When these assumptions are not met, incorrect predictions can be generated. For instance, in an age-structured population, the intrinsic growth rate does not predict the rate of evolutionary change if the assumption that selection is weak is violated. Hamilton's rule can be broken when there is dominance ($h \neq 1/2$). In short, defining appropriate fitness functions can provide a short-cut, helping us to predict quickly and easily the outcome of evolution. Yet these predictions are only as valid as the genetic models from which they were derived. Nevertheless, they are often a useful first step, especially since the genetic architecture of many traits remains unknown.

One goal of evolutionary biology is to understand and predict the outcome of natural selection. In the simplest of cases, fitness estimated for each type over a specified length of time may be sufficient for making these predictions. In more complicated scenarios, alternative measures of fitness, such as the geometric mean fitness, may prove more useful. It must always be kept in mind that evolution involves the interplay of many forces and factors. Although the viability and fertility interpretation of fitness is the most general, understanding the long-term outcome of evolution will usually be more difficult than simply looking for the type with the highest fitness. That the majority of species that have ever inhabited Earth are now extinct serves to remind us of this fact.

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Further Reading

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