**Fitness**

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**Synonyms**

Adaptation; Direct and indirect fitness; Inclusive fitness; Individual genotype growth; Kin selection; Leslie matrix; Lifetime reproductive success; Survival

**Definition**

*Fitness*: the change in frequencies of alternative forms of an organismal trait over time in a population. Change can be within a generation, in which case transmission to the next generation depends on genetic and nongenetic inheritance, or among generations, in which case inheritance is implicit.

**Introduction**

Fitness is central to Darwin’s theory of evolution by means of natural selection, and the concept of fitness is intimately tied to that of adaptation (Darwin 1859; Fischer 1930). What Darwin called the “struggle for existence,” later referred to as “survival of the fittest” by H. Spencer (1866), is the idea that the *fittest entities* in nature are those best *adapted* to prevailing environmental conditions. Fit entities are better at surviving and reproducing in given environments, spreading higher numbers of copies of their characteristics (or, rather, traits) through generations and in the population. The above highlights three important points:

1. Natural selection acts on entities that exhibit variations in traits (i.e., different forms of those traits) that can be passed on from parents to offspring. It is *heritable trait forms* (not necessarily genetic) that lead to greater overall fitness of individuals, and it is the trait forms that endure through generations and spread or decline in the population.

2. Fitness depends on the environment. A trait form can be adaptive (conferring high fitness) in a given environment but maladaptive (conferring low fitness) in another.

3. Darwinian fitness is a *relative*, frequency-based measure, that is, characteristic of a population of individuals. It is the fitness of a given trait form relative to others that matters to the individuals that carry the trait form. This is because natural selection operates in terms of changes in frequencies, not absolute numbers.
(Poulton 1884; Clarke 1979). Thus, the key concept of fitness for natural selection is the “fitness difference” among alternative forms of a trait (Endler 1986).

Defining and refining the concept of fitness has been an ongoing exercise in the field of evolutionary ecology (Hamilton 1964; Caswell 1980; Grafen 1982, 1984; Lucas et al. 1996; Queller 1996; McGraw and Caswell 1996; Hunt and Hodgson 2010). Here, we provide a condensed overview of the concept for graduate students, academics, and practitioners.

**Unit of Selection in Defining Fitness**

Most evolutionary biologists view fitness as the property of an entity that is a biological characteristic of individuals: a genotype or group of genes (Hamilton 1964; Williams 1966; Grafen 2009). Successful genotypes under selection have high fitness and will proportionally increase at a higher rate in the population. A problem from this general viewpoint is that each genotype is unique and is diluted by inheritance, since only half of a genotype can usually be passed on to offspring. An alternative viewpoint is that selection occurs at the level of the single gene (Dawkins 1976). In this case, the individual phenotype – and its interactions with the environment – is viewed as a competitive vehicle shaped by the gene (and its interaction with other genes), to ensure the gene’s journey through generations to immortality (Dawkins 1976, 1982). Here, fitness is theoretically measured at the level of the gene (Gardner and Welch 2011). However, this concept also appears impractical, since most phenotypic traits in real-world organisms are governed by the additive effects of an infinite number of loci distributed all over the genome, each having an infinitesimally small effect on a character (Hill and Kirkpatrick 2010). As emphasized by Mameli (2004), one issue with current views of evolution is the premise that natural selection acts on genetic variation or genetically caused variation. Yet, the modern evolutionary synthesis is currently undergoing a profound paradigm shift with growing evidence that not all forms of inheritance are genetic, and evolutionary models need to account for both sources of genetic and nongenetic inheritance in predicting evolutionary change (Helanterä and Uller 2010; Danchin et al. 2011; Danchin 2013). An example of nongenetic inheritance is maternal care behavior (licking and grooming) in rodents (Champagne 2008). Maternal care behavior is related to variation of specific (epigenetic) factors that modify the expression (not the DNA sequence) of given genes, themselves related to the expression of maternal behavior (Weaver et al. 2004; Champagne 2008). Such epigenetic trait forms may be passed on through generations with important implications for how we think about natural selection (Danchin 2013).

Because trait variation (whether anatomical, physiological, behavioral) is shaped by heritable sources of variation that are both genetic and nongenetic, fitness differences are likely best measured at the level of the phenotypic trait – integrating all sources of phenotypic variation. Empirically, this approach further provides the advantage of practicality, since measuring phenotypic characters (e.g., height) is straightforward and does not require making assumptions about the genetic and nongenetic architecture underlying trait variation. Measuring selection on traits often makes the assumption that traits are independent with respect to change between generations, disregarding the fact that some traits coevolve or are genetically (or nongenetically) linked (Falconer 1981; Lande and Arnold 1983; Charmantier et al. 2014). However, refinements in statistical methods and computing algorithms are progressively allowing us to parse out sources of variation underlying phenotypic traits (Kruuk 2004; Kruuk and Hadfield 2007), including between correlated traits (Lane et al. 2011; Bize et al. 2017). Those models provide promising avenues for understanding the importance of genetic and nongenetic sources of variation in evolution (Charmantier et al. 2014).
A Caveat: Inclusive Fitness

One of the most significant advances in defining Darwinian fitness came from Hamilton (1964) and his concept of inclusive fitness. First advanced by Darwin (1859), and later discussed by Fischer (1930) and Haldane (1932), Hamilton laid out the mathematics for explaining how apparently altruistic behavioral traits might evolve, i.e., traits favoring the reproduction of others at a cost of one’s own reproduction and survival. Such an evolutionary strategy, termed kin selection by Maynard Smith (1964), results if the net fitness benefits of expressing cooperative or helpful traits, weighed by the degree of relatedness to the helped individual, outweigh the costs suffered by the helper. This breaks fitness into direct and indirect components, inclusive fitness being the summation of the two. An indirect component to fitness due to helping behavior comes about according to Hamilton’s rule: $rB - C > 0$. Here, $B$ is the fitness benefit of the cooperative behavior to the recipient, $C$ the fitness cost of the behavior the donor, and $r$ the degree of relatedness between the donor and recipient (not the intrinsic rate of natural increase of a population, but unfortunately given the same symbol). Inclusive fitness reduces to direct fitness when there is no helping behavior, that is, when the indirect component is zero. A similar argument can be applied to behaviors that appear spiteful: behaviors that hinder unrelated individuals more than kin (Dobson et al. 2000; West and Gardner 2010).

Measuring Fitness in Practice: Annual Measures

As a practical matter, fitness differences among alternative forms of a trait can only be measured from the reproductive success of the individuals that exhibit the particular trait forms. Reproduction and survival each contribute to the number of successful offspring that individuals with a particular trait form produce. Thus, if we ignore the effects of genetic (and epigenetic) architecture, the task seems fairly simple: simply add up the number of offspring that each individual produces and average individuals that exhibit each trait form. The point is to use the success of individuals relative to others to estimate the fitness of trait forms.

The simplest measure of fitness in an experiment, or in populations where individual life histories are known (e.g., annual schedules of reproduction and survival), is to consider individual annual reproductive success and individual annual survival separately as components of fitness. More comprehensively, both measures can be combined by counting the number of gene copies present in a population from 1 year to the next, for each individual in the population (Qvarnström et al. 2006). For example, this approach was used in common terns, *Sterna hirundo*, where the timing of egg laying was studied with respect to annual number of fledglings, annual survival to the next year, and a combined annual fitness measure (Dobson et al. 2017). The annual fitness measure was the number of individual gene copies surviving to the next year: for a given individual, this represented half the number of the fledglings it produced (because young carry half of each parent’s genes), plus its survival to the next year (0 or 1). Perhaps the most comprehensive approach to measuring annual fitness is to consider both the combined fitness measure and concurrently break it down into its fecundity and survival components (see also Raveh et al. 2015).

Measuring Fitness in Practice: Lifetime Measures

The drawback of annual and shorter-term fitness measures is that they do not account for effects that last longer during the lifespan. For example, an advantageous environment during an individual’s developmental period can lead to improved reproduction and survival over the lifetime (for an example in bighorn sheep, *Ovis Canadensis*, see Pigeon et al. 2017). Capturing such effects requires working at the scale of an individual’s lifetime. This is termed “lifetime reproductive success” or LRS, and it has been extensively applied (we know of no detailed review, but a
search of the Web of Science for the term “lifetime reproductive success” brings up about 1000 articles at the time of writing). While it would be preferable to measure offspring production as those that go on to reproduce themselves, offspring production is most often measured at an earlier stage (such as eggs laid or juveniles produced), usually because of the complexity in natural history studies to tease apart whether juvenile disappearance from the population is due to emigration or death.

Lifetime reproductive success suffers from an important drawback: fitness differences depend on the timing of reproduction, not just the number of offspring. Timing is especially important for organisms with long lifespans, so that survival becomes a critical aspect of any measure of fitness (e.g., in seabirds; Jouventin and Dobson 2002; Reed et al. 2008). Reproduction cannot occur without survival to reproductive age, the number of times that an individual reproduces requires extended survival, and the rapidity of offspring production may itself influence survival patterns. For all of these reasons, two measures of fitness have been commonly used, net reproductive rate (usually symbolized as R₀) and the intrinsic rate of population increase (symbolized as r or the related \( \lambda = e^r \), \( \lambda \) is called the “finite rate of population increase”) (de Jong 1994). These practical measures are applied to subgroups in a population in which individuals express alternative forms of a trait. \( R_0 \) is not standardized by generation time, which might differ among different trait forms. Thus, \( r \) or \( \lambda \) are preferred fitness measures that take the timing of reproduction into account (Stearns 1992).

The usual procedure is to separate a population into groups representing alternative trait forms and then treat the groups as though they were independent populations themselves. Life tables with information on reproduction and survival are commonly used to calculate rates of population growth, assuming that vital rates will not change. A life table can also be constructed for individuals, treating each individual as a population that exhibits the trait form (for examples of individual fitness at different ages at maturity in sparrow hawks and blue tits, see McGraw and Caswell 1996). The reproductive rate is simply the reproduction for the individuals, and the survival rate is 100% throughout life. A measure of population growth such as \( \lambda \) can then be calculated from an algebraic matrix that reflects the individual’s success at reproduction and survival. Individuals with different trait forms are then averaged as separate subpopulations within the larger population. The alternative trait form with the greater average \( \lambda \) value is judged to have greater fitness and thus at an advantage during natural selection.

The individual matrix approach (McGraw and Caswell 1996; Oli and Armitage 2008; Viblanc et al. 2010) uses individuals to estimate the fitness benefits of different forms of the trait and should provide a good comparison of alternative trait forms, if all individuals lived the same lifespan and were born in the same year. In real populations, however, individuals are often born at different times. This leads to a problem, because individual fitness measures will be higher when a population is growing and lower when a population is declining. Because natural selection produces changes in gene frequencies, fitness must be considered relative to what others in the population are doing. In an increasing (or decreasing) population, an individual with an individual fitness value of 1.0 is below (or above) average, and the trait forms that the individual carries will decline (or increase) in frequency. The solution to this problem is methodological: one should take changes in population size into account. This can be done by comparing individual fitness to how the population is changing during the lifetime of the sampled individuals. For instance, in Columbian ground squirrels (Urocitellus columbianus), changes in population size during each individual’s lifetime were used to calculate an “individual” estimate of population change over the lifespan (Viblanc et al. 2010). In an unpublished study (Dobson et al., manuscript), individual fitness was also compared to changes in population size during an individual’s lifetime using a traditional “Leslie matrix” measure of population growth (after Leslie 1945; for details of methodology, see Caswell 2001). In both approaches, individual fitness estimates can then be adjusted
for population growth during the individual’s lifetime using regression analyses to provide an individual fitness estimate that is stripped of the influences of changes in population size.

**Return to the Inclusive Fitness Concept**

The above annual and lifetime practical fitness measures are suitable for traits when there is no indirect component to inclusive fitness. But if the traits influence the success of other individuals, such as close kin, then additional care is necessary. In a study of fitness effects of the presence of close kin in cooperative females of the Columbian ground squirrel, an attempt to estimate inclusive fitness and its direct and indirect components was made (Dobson et al. 2012). The specific behavioral traits were estimated from the presence or absence of female close relatives in this matrilocal species, but evidence suggested that the beneficial trait was the propensity or rate of aggressive behavior. Individual fitness measures relative to population size were calculated as described above for 70 females (after Viblanc et al. 2010).

The major difficulty for calculating direct and indirect components of individual fitness is to count each fitness component only once (Grafen 1982; Creel 1990; Lucas et al. 1996; Queller 1996). Hamilton (Hamilton 1964, well explained by Oli 2003) described a process of “stripping away” the effects of help so that they are singly counted. In practice, the direct component of fitness can be estimated from females that have no close kin nearby that can help them. For the indirect component, it is necessary to estimate the individual fitness of females that received help and subtract (strip) away the estimate of direct fitness, leaving the residual fitness due to the help of their relative. When this procedure was applied to ground squirrels, the direct component of fitness accounted for about 60% of a female’s estimated fitness and the indirect component the other 40%. This result suggests that individual fitness was much higher when helping was present, and significant differences in the actual fitness estimates bore this out. This example shows the advantage of studying the fitness of trait forms, even when the basis of genetic variation is unknown or in question. If genetic variation in helping behavior had been present, it would have had a strong fitness advantage.

**Caveat Emptor**

Fitness is a complicated topic because it applies to trait forms, but can most easily be measured from the individuals that carry the trait forms. And this is “fitting,” since it is the individuals that survive and reproduce. But this means that each trait form is embedded within the other traits that the individuals exhibit. Thus, when there are interactive effects among trait forms, as is likely, current methods of measuring fitness will have to be modified. Current models of natural selection take associations and interactions among trait forms into account by examining a genetic variance-covariance matrix for the traits involved (Houle 1991; Steppan et al. 2002). Thus, in the future, the fitness of individual trait forms may have to be modeled within a matrix of organismal traits, as well as for its genetic and nongenetic components.

**Cross-References**

- Additive Genetic Variance
- Alleles
- Allelic Association
- Artificial Selection
- Behavioural Variation
- Charles Darwin
- Coevolution
- Convergent Evolution
- Directional Selection
- Divergent Evolution
- DNA
- Evolution
- Fisher
- Frequency Distribution of Phenotypes
- Frequency-Dependent Selection
- Gene Flow
- Gene Frequency
- Gene Pool
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