

Fitness and Variance

Brad Weslake
NYU Shanghai
<http://bweslake.org/>

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Introduction

The Question

- ▶ **The Question:** What is fitness?
- ▶ **The Question is Non-Trivial:**
 - ▶ There is an enormous amount of variation in the definitions of fitness employed by biologists.
 - ▶ Some of this variation is benign, reflecting different fitness concepts (eg. long term vs short term fitness, absolute vs relative fitness), or different informal textbook definitions.
 - ▶ But some of this variation reflects genuine disagreement, since the definitions figure in attempts to state the general conditions required for natural selection to occur.
 - ▶ Moreover many of these definitions are demonstrably incorrect, in the sense that they fail to cover all of the cases in which measures of fitness are actually employed.

Two Kinds of Answer

- ▶ **Fitness is Unified.** A single definition of fitness:
 - ▶ From which all other fitness concepts can be derived.
 - ▶ That can figure in an account of the general conditions required for natural selection to occur.
- ▶ **Fitness is Disunified.** There is no such definition.

It is better to say, instead, that there is a family of fitness-like or fitness-related properties, all involving reproductive output in some sense or other. Different ones are relevant in different circumstances, and this shows up in the diverse fitness-related properties seen in different formal models (Godfrey-Smith 2009).

Plan

Aim

- ▶ Show how one common definition of fitness fails to cover an important class of cases.
- ▶ Argue, on the basis of these cases, that we should reject a common assumption about the relationship between the fitness of individuals and the fitness of types.

Structure

- ▶ Historical Background
- ▶ The Propensity Interpretation of Fitness
- ▶ Fitness and Variance in Reproductive Success
- ▶ Fitness is not Fundamentally a Property of Individuals

Historical Background

Darwin

- ▶ The term “fitness” appears only *once* in the 1st edition of the *Origin* (1859).
- ▶ The phrase “survival of the fittest” didn’t appear until the 5th edition of the *Origin* (1869). It was borrowed from Herbert Spencer (1864), at the urging of Alfred Russel Wallace (Paul 1988).
- ▶ While various other cognates of the term appear, they are always used to describe the fit between an organism and an environment: what Darwin elsewhere refers to as “adaptation”.

Population Genetics

- ▶ Fitness introduced to population genetics by Fisher (1930).
- ▶ While Fisher sometimes uses the term in Darwin's sense, he also explicitly uses it to label the relative rate of increase or decrease of a type in a population.

In Sum:

- ▶ Fitness was originally used to describe the fit between an organism and environment, but *also* came to be used to describe any measure of the rate of increase of a type in a population.
- ▶ These are what Sober calls the “two faces” of fitness:

Fitness is both an ecological descriptor and a mathematical predictor (Sober 2000).

The Propensity Interpretation of Fitness

The Propensity Interpretation

- ▶ Proposed by Brandon (1978) and Mills and Beatty (1979).

1. **Propensity.** Fitness is a propensity.
2. **Uniformity.** Fitness has a single measure.
3. **Offspring.** Fitness is measured by expected offspring number.
In particular, the absolute fitness of an organism O in environment E can be represented as:

$$\sum_{i=0}^{\infty} P(Q_i^{OE}) Q_i^{OE}$$

where Q_i^{OE} is a number representing O having i offspring in environment E , and $P(Q_i^{OE})$ represents the probability of O having i offspring in environment E .

4. **Priority.** The fitness of a type is grounded in the fitnesses of individuals of that type.

Priority

- ▶ **Priority.** The fitness of a type is grounded in the fitnesses of individuals of that type.
 - ▶ Obviously, the fitness of a type is grounded in the collective reproductive success of the individuals of that type. **Priority** expresses a more specific claim: that the fitness of a type is grounded in the *fitnesses* of the individuals of that type.
 - ▶ Since fitnesses are measured by numbers, this entails that there is a mathematical function from the fitnesses of the individuals of a type to the fitness of the type.
 - ▶ For example, Mills and Beatty (1979) propose that the absolute fitness of a type is the *average* of the absolute fitnesses of individuals of that type.

Fitness and Variance in Reproductive Success

Between Generation Variance

- ▶ **Definition.** All individuals of the same type have the same number of offspring in any given generation, but there is variation in offspring number between generations.
- ▶ **Example.** Asexual synchronised reproduction, parents die upon reproducing. Two **A** and two **B** individuals. **A** individuals have probability 1 of having 2 offspring: $p(A_2) = 1$. **B** individuals have $p(B_1) = \frac{1}{2}$ and $p(B_3) = \frac{1}{2}$.
 - ▶ The *expected total offspring number* is identical:
 $(2)(2) = (\frac{1}{2})(2) + (\frac{1}{2})(6) = 4$.
 - ▶ But the *expected frequency* is different:
Expected frequency of **A**: $(\frac{1}{2})(\frac{4}{6} + \frac{4}{10}) = 0.535$
Expected frequency of **B**: $(\frac{1}{2})(\frac{2}{6} + \frac{6}{10}) = 0.465$
- ▶ **Measure.** The fitness of type A_i is $\mu_i - \frac{1}{2}\sigma_i^2$, where μ_i is the mean number of offspring of type A_i and σ_i^2 is the variance in the number of offspring of type A_i (Gillespie 1973).

Within Generation Variance

- ▶ **Definition.** There is independent variation in offspring number between individuals.
- ▶ **Example.** Asexual synchronised reproduction, parents die upon reproducing. Two **A** and two **B** individuals. **A** individuals have $p(A_2) = 1$. **B** individuals have $p(B_1) = \frac{1}{2}$ and $p(B_3) = \frac{1}{2}$.
 - ▶ The *expected total offspring number* is identical:
 $(2)(2) = (\frac{1}{4})(2) + (\frac{1}{2})(4) + (\frac{1}{4})(6) = 4$.
 - ▶ But the *expected frequency* is different:
Expected frequency of **A**: $(\frac{1}{4})(\frac{4}{6} + \frac{4}{8} + \frac{4}{8} + \frac{4}{10}) = 0.52$
Expected frequency of **B**: $(\frac{1}{4})(\frac{2}{6} + \frac{4}{8} + \frac{4}{8} + \frac{6}{10}) = 0.48$
- ▶ **Measure.** The fitness of type A_i is $\mu_i - \frac{1}{n}\sigma_i^2$, where n is population size (Gillespie 1974).

Lessons

- ▶ The measures of fitness formulated by Gillespie (1973; 1974) show that **Offspring** is false. For they entail the possibility of fitness *differences* in populations of types which have the *same* expected offspring number.
- ▶ One response to this is to retain the other three claims that make up the propensity interpretation, but amend the measure of fitness:

We view this as a problem concerning the appropriate measure of fitness, not its definition (Richardson and Burian 1992, 359).

These counterexamples are problems not with the [propensity interpretation] itself, but with the various mathematical models of it which have been proposed (Pence and Ramsey 2013, 875).

Fitness is not Fundamentally a Property of Individuals

Within Generation Variance and Priority

- ▶ As Sober (2000) points out, it is an implication of the Gillespie (1974) fitness measure for the case of within generation variance that *the fitness of a type can be changed without changing the reproductive propensities of any individuals of that type*.
- ▶ This is because of the role of n , which represents population size. In our example, the fitness of type **A** can be changed by changing the population size. This in turn can be changed by simply changing the number of **B** individuals.
- ▶ We should therefore conclude that **Priority** is false.

Objection I

- ▶ *Objection:* n makes a difference to the reproductive propensities of individuals, because populations must be composed of causally interacting individuals (Millstein forthcoming).
- ▶ *Reply:* The fact that populations must be causally connected doesn't entail that n makes a difference to the reproductive propensities of individuals.

Objection II

- ▶ *Objection:* n plays an eliminable role in the measure of fitness (Otsuka et al. 2011).
- ▶ *Reply:* n can be eliminated only if it is replaced by a measure according to which the fitness of type A_i is $\mu_i - q_i \rho_i \sigma_i^2$, where q_i is frequency and ρ_i is correlation in reproductive success (Frank 2011). But as with population size, frequency and correlation can be changed without changing the reproductive propensities of individuals.

Objection III

- ▶ *Objection:* We can save **Priority** if we give up **Propensity**, by allowing that the fitness of *individuals* also depends on n (Sober 2000).
- ▶ *Reply:* n is *irrelevant* to the reproductive success of individuals, so should not be incorporated into any measure of individual fitness.

An Upshot

- ▶ There are two forms of density dependent selection, and two forms of frequency dependent selection:
 - ▶ The dependence may be *causal*: population size or frequency may influence expected frequencies by causing differences in reproductive propensities.
 - ▶ The dependence may be *non-causal*: population size or frequency may influence expected frequencies as a consequence of mathematics alone.
- ▶ Failure to distinguish these has obscured the real lessons of variance in reproductive success.

Conclusion

- ▶ Cases involving variance in reproductive success entail that **Offspring** is false, as a measure of the fitness of types.
- ▶ I have argued that they also entail that **Priority** is false.
- ▶ For all I have said, **Uniformity** and **Propensity** may be true. Indeed, individual fitness may be a propensity measured by expected offspring number, and type fitness may be a propensity measured in some different uniform way. What would nevertheless be false is that there is a function from the one to the other.

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