Two Fitness Fallacies

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Reasoning about fitness can be tricky. Below are two mistakes to avoid. For a third, see the discussion in Sober (2011, chapter 3) on how Darwin reasoned about sex ratio.

1. What is the probability relation between fitness and actual reproductive success?

Most philosophers of biology agree that fitness cannot be equated with actual reproductive success. It's a probabilistic quantity. How, then, are fitness and actual reproductive success related? A standard answer (Brandon 1978; Mills and Beatty 1979; Sober 1984; Rosenberg and Bouchard 2008) is the following:

(*) $w_f(A) > w_f(B)$ iff A probably has more offspring than B.

The "f" subscript indicates that we now are talking about fertility, not viability. For the sake of simplicity, let A and B individuals have the same viabilities. Proposition (*) can be regarded as a claim about two token individuals or about two traits.

This biconditional is mistaken, as the example described in the accompanying table illustrates. Trait A has a larger expected number of offspring than trait B, so A is fitter if we measure fitness by expected number of offspring. But what is the probability that an A individual will have more offspring than a B? The probability of this is only $(0.1) + (0.9)(0.1) = 0.19$, which means that the probability is 0.81 that the B individual will have more babies. The argument just stated pertains to two token individuals, but it also applies to traits. Consider a large population in which there are equal numbers of A and B individuals. Randomly form those individuals into AB pairs. In 81% of those pairs, the B individual out reproduces the A.

Traits	Each trait's probabilities of having how many offspring		Expected number of offspring
	0.9	0.1	
A	2	100	$1.8 + 10 = 11.8$
B	3	1	$2.7 + 0.1 = 2.8$

There is nothing "fancy" about this counterexample to proposition (*). We aren't talking about a trait like sex ratio, in which expected number of offspring is the wrong measure because we need more than a next-generation look ahead to define the fitness concept (Sober 2001). Nor are we talking about cases of the sort described by Gillespie (1977) in which fitnesses do not go by arithmetic expectations.

2. The sample path fallacy

No one would buy the following argument for why fitness cannot be identified with expected number of offspring:

> Let *A* have a 0.5 probability of having 1 offspring and a 0.5 probability of having 3 (so *A*'s expected number of offspring is 2). Let the same be true of *B*. Now suppose that *A* in fact has 1 offspring and B has 3. Since they differ in their actual reproductive success, fitness can't be identified with expected number of offspring.

The flaw in this argument is that it attends to just one sample path – the one in which *A* has 1 offspring and B has 3. There are three other possibilities, which need to be considered as well, with due attention to their probabilities.

Unfortunately, this style of argument has been used to explain Gillespie's (1977) idea that variance needs to be included in the characterization of fitness (Beatty and Finsen 1989; Brandon 1990; Rosenberg and Bouchard 2008). Suppose, for example, that the *A* individuals in a generation each have 2 offspring and that the *B* individuals in a generation either all have 1 offspring or all have 3, with equal probability.[1] Which trait is fitter? Here is a fallacious argument:

> Suppose the population begins with 10 *A*s and 10 *B*s and that *B*'s productivity alternates between 3 and 1 in a sequence of generations. Then (assuming that the parents die after they reproduce), the numbers of *A* and *B* individuals in the next nine generations will be the ones shown in the accompanying table. *A* and *B* start with frequencies of 0.5, but A increases in frequency. Therefore, *A* is fitter. So fitness is not identical with expected number of offspring.

This argument considers only one sample path for *B*. In fact, for 10 generations there are 2^9 sample paths. Why focus on the one in which the productivities of *B* are 3-1-3-1-3-1-3-1-3 rather than on the sample path 3-3-3-3-3-3-3-3-3? They have the same probability. It may be replied that the alternating sample path is "typical" whereas the all-3 sample path is not, and that

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[1] In this example, all the variance in B's reproductive output is between generations. Gillespie also analyzes the case where all the variance is within generations.

the description of a single sample path is meant to be heuristic, not demonstrative. Maybe so, but what would a more rigorous explanation look like?

Generation		1	2	3	4	5	6	7	8	9	10
Traits	A	10	20	40	80	160	320	640	1280	2560	5120
	B	10	30	30	90	90	270	270	810	810	2430

To think about the fitnesses of the two traits, we need to consider *all* the sample paths. But what number should we compute? If we compute the expected number of A and *B* individuals after, say, 10 generations, the answer is that the two traits are the same – each has 5120 as its expected value. To see this point, consider the two simplest cases:

- In the 2nd generation, there are 20 *A*s and either 10 or 30 *B*s with equal probability, so the expected number of *B*s in the 2nd generation is 20.

- In the 3rd generation, there are 40 *A*s and either 10 or 30 or 30 or 90 *B*s, with equal probability, so the expected number of *B*s is 40.

The pattern does not change if we consider the 4th or 5th or n^{th} generation. Gillespie's argument does not involve computing the expected number of offspring of the two types and claiming (falsely) that the trait with the lower variance has the higher expected number of offspring. Rather, it involves computing the expected *frequencies* of the two traits. The expected frequency of *A* after even one generation (when the two traits begin at 50/50) is greater than that of *B*. After one generation, there are 20 *A*s and either 10 or 30 *B*s with equal probability, so the expected *frequency* of A in the 2nd generation is ½(20/30 + 20/50) = ½(0.67 + 0.4) = 0.535. Fitness needs to reflect the variance as well as the arithmetic expectation because fitnesses are used to predict trait *frequencies*. If the job of fitness were merely to calculate expected number of offspring, there would be no argument against defining fitness as expected number of offspring (a tautology).

References

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