The Unity of Fitness

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Abstract

It's been argued that fitness cannot always be defined as expected number of off-spring; different, more complex functions are required for different contexts. Brandon (1990) argues that fitness therefore merely satisfies a common schema. Other authors (Ariew and Lewontin, 2004; Krimbas, 2004) argue that no unified mathematical characterization of fitness is possible. I focus on comparative fitness, explaining that though comparative fitness must be relativized to an evolutionary effect which fitness differences help cause, thus relativized it can be given a unitary mathematical definition in terms of probabilities of producing offspring of various types and various other effects. Fitness will sometimes be defined in terms of probabilities of effects occurring over the long term, but I argue that these probabilities nevertheless concern effects occurring over the short term.

1 Introduction

According to the original version of the propensity interpretation of fitness (PIF) (Brandon, 1978; Mills and Beatty, 1979), biological fitness is a mathematical function of probabilities and numerical values associated with reproductive outcomes, i.e. expected number of offspring. This approach seems to take fitness to be a real aspect of the process of natural selection, an aspect which is approximated by various fitness and selection coefficient terms in models of selection, drift, etc. In response to work by Gillespie (1973; 1974; 1975; 1977), some authors have argued that fitness should sometimes be defined in terms of a more complex function (Beatty and Finsen, 1989; Brandon, 1990; Sober, 2001). Brandon (1990) argued that fitness therefore merely satisfies a common schema instantiated by different mathematical functions More extreme conclusions have been drawn from arguments that fitness must sometimes be characterized by an even wider variety of mathematical functions because of conspecifics' mutual influence on reproductive success (Ariew and Lewontin, 2004; Krimbas, 2004). Despite the heterogeneity of mathematical functions needed to *model* fitness, I argue for the following.

As a causal and explanatory factor, fitness must be relativized to an effect or explanandum to be caused/explained, but as long as the effect is carefully specified, there is a single, often simple, mathematical property which constitutes the fact that one type is fitter than another. In particular, for questions about what caused one type or another to be better represented at the end of an interval of time, a type A is fitter than another type B iff A has a greater probability of having increased its frequency more than B at the end of that interval.

Though in such cases fitness must be defined in terms of probabilities of reproductive effects over several generations, I argue that fitness nevertheless has to do with influence in each generation. Since probabilities of long-term effects can be derived from probabilities of short-term effects, the former are simply mathematical properties of causes acting in the short term. These short-term mathematical properties will often be difficult or impossible

to discover with any precision; that is why they must be modeled by a variety of relatively simple approximations.

PIF advocates usually claim that the probabilities of which fitness is a function are propensities, a (proposed) kind of indeterministic disposition. One can criticize this aspect of the PIF by criticizing the concept of propensity generally,[1] or by arguing that if propensities exist, their behavior doesn't allow them to play the role that the PIF requires (Abrams, 2007a). Such "Function of what?" problems might be solved by arguing that some other kind of probability plays the appropriate role. I'll ignore this kind of problem here, simply assuming for now that appropriate probabilities—whether propensities or something else— do exist.

My focus will instead be on what I call the "What function?" problem. This arises from the question of what mathematical function of probabilities and other factors fitness might be, and arguments that there is no one function common to all contexts in terms of which a central notion of fitness should be defined. Sections 2–4 concern "What function?" problems raised by Gillespie's work (Gillespie, 1973, 1974, 1975, 1977; Beatty and Finsen, 1989; Brandon, 1990; Sober, 2001) . Section 5 addresses "What function?" challenges raised by Krimbas (2004) and Ariew and Lewontin (2004).[2]

I'll assume that in the final analysis, the kind of fitness relevant to natural selection is fitness of *types*, i.e. properties of organisms, since it is types that are heritable and selected for. Fitness is often attributed to token organisms, but marginal fitnesses of various heritable types can then be derived by averaging (e.g. Mills and Beatty, 1979; Sober, 1984b, 2001; Ewens, 2004; Rice, 2004).

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[1](Eagle, 2004) surveys criticisms of propensity concepts.

[2]My responses to the "What function?" challenges raised by Krimbas and Ariew and Lewontin actually involve an answer to a "Function of what?" question, in particular the question of what sorts of outcomes the probabilities constitutive of fitness concern.

2 Troubles with expectationalism

As mentioned above, the original PIF defined fitness as the expectation or arithmetic mean of the number of offspring:

$$\text{Fitness of } A = \sum_{i=0}^{\infty} i \, \mathsf{P}(O_A = i) \, ,$$

where "$O_A = i$" says that an organism of type A has i offspring.[3] However, PIF advocates (Beatty and Finsen, 1989; Brandon, 1990; Sober, 2001) and others have questioned the original PIF because of Gillespie's arguments (1973; 1974; 1975; 1977) that a type with a lower expected number of offspring than another can have a greater probability of long-term reproductive success. This can happen because the number of organisms of a given type in one generation is in part a function of the number of organisms previously producing offspring of that type. This means that the overall shape of the probability distribution over numbers of offspring, not just its mean, is relevant to long-term evolution. In very simple cases, the most probable outcome of competition between two types A and B over a large number of generations n is that A will increase its frequency in the population iff its geometric mean number of offspring is greater than B's:

$$\prod_{i=0}^{\infty} i^{\mathsf{P}(O_A=i)} > \prod_{i=0}^{\infty} i^{\mathsf{P}(O_B=i)}$$

In a short discussion (Gillespie, 1977) of his earlier work (Gillespie, 1973, 1974, 1975), Gillespie pointed out that in some simple cases, we can approximate a predictive measure of fitness using certain functions of expectation and variance. Philosophers have as a result sometimes focused on variance as *the* mathematical property other than expectation which

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[3]I suspect that writers on fitness sometimes forget that "expect" and "expectation" have no psychological or predictive connotation in themselves. Thus one should not necessarily expect the "expected value" to occur, e.g. for a bimodal distribution. (Consider drawing a ball from an urn with 1000 balls labeled "1", one labeled "2", and 1000 more balls labeled "3".)

is relevant to fitness (Brandon, 1990; Sober, 2001). However, Gillespie's claims about variance only concerned certain cases, and careful reading of some of Gillespie's papers shows that complex functions of higher statistical moments would be needed to provide a precise definition of fitness in such cases.[4] Beatty and Finsen (1989) gave an example in which the third moment (skew) of two offspring distributions made a difference to fitness. The distributions for A and B below have the same arithmetic mean, variance, and skew, but B's fourth moment (kurtosis) is greater and its geometric mean is smaller. The fact that B's geometric mean is slightly smaller shows that in experiments over several generations, A would usually outreproduce B:

# offspring:	1	2	3	4	5	arith. mean	variance	skew	kurtosis	geom. mean
probability for A:		.2	.6	.2		3.0	.4	0	.4	2.930
probability for B:	.05		.9		.05	3.0	.4	0	1.6	2.913

Moreover, for some cases, Gillespie's analyses begins with approximating assumptions, so no claim about what precise function fitness is would be implied.

Beatty and Finsen (1989) and Brandon (1990) considered defining fitness in terms of long-term measures of success such as geometric mean number of offspring, Cooper's (1984) expected time to extinction, and Thoday's (1953) probability of persistence 10^8 years. Brandon, however, argued that fitness can't be defined by a long-term measure, because fitness differences are supposed to reflect causes of evolution, and causes produce their effect over (many) short-term periods: "Selection has no foresight; it has no means to discriminate among organisms based on their long-term probability of having surviving offspring" (p.

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[4]For example, it's mentioned in the discussion at the bottom of page 1012 of (Gillespie, 1977) and it's implicit in the derivation of equation (7) on page 1013 that higher statistical moments can be relevant to relative reproductive success. Gillespie argues that these moments typically make a small contribution to fitness. He's surely correct in this, but that doesn't mean that higher moments never matter in practice, and they certainly matter in principle.

25). No doubt because mean and variance seem like respectable short-term properties, and because Gillespie's summaries used them, Brandon argued that fitness should be defined by various functions of mean and variance in different contexts. In response, Sober (2001, p. 313) remarked that "long-term probabilities imply foresight no more than short-term probabilities do", but he gave little explanation of this remark. Sober also gave examples which suggested that both short-term and long-term fitness measures might be useful. I agree with both of Sober's points, but I think that they can be further clarified and can be given a more systematic foundation. This is part of what I try to do below.

3 Long-term short-term fitness

Notice that the worry that prompted Beatty and Finsen and Brandon to revise the original expectation-based definition of fitness was that expected number of offspring sometimes didn't correspond to probable *long-term* success. Long-term success is clearly what matters in some contexts. Moreover, Gillespie's results, on which these authors had focused, were actually of measure of fitness in terms of probable long-term success—*approximated* with simple statistical functions such as expectation and variance. Also notice that an apparently long-term measure like geometric mean in fact just captures a mathematical fact about a short-term probability distribution over numbers of offspring. Even expected time to extinction or probability of persistence 10^8 years can be considered mathematical property of short-term probability distributions over numbers of offspring: *Probabilities of changes in frequencies over the long term are implied by short-term reproductive probabilities* and probabilities of other short-term probabilities. Let me explain.

To fix ideas, here is a relatively concrete example. Suppose we have a population of 3 A's and 2 B's and that reproduction is seasonal and asexual. For each number of offspring there is a probability of producing that many offspring by an A, similarly for a B. There

are several possible states of the population in the next generation, e.g. 6 A's and 4 B's; 0 of A and 1 of B, or 2 of B, or 3, or 4; extinction of the population; and so on. Each state can result from the A's and B's producing numbers of offspring which add up to the numbers of A's and B's corresponding to that state. Each state's probability is thus implied by probabilities of numbers of offspring. The same is true for more complex examples.

More generally, at each generation there is a set of transition probabilities $\mathsf{P}_1(j|i)$, probabilities the population will go into state j one generation later given state i in the current generation. These 1-generation transition probabilities imply multiple-generation transition probabilities.[5] For example, the probability of going from i to k two generations after the current generation is the sum, over all intermediate states j, of probabilities of going to j and then into k:

$$\mathsf{P}_2(k|i) = \sum_j \mathsf{P}_1(k|j)\, \mathsf{P}_1(j|i)$$

Notice what this means: Short-term probabilities of numbers of offspring imply probabilities of frequencies many generations later.[6] Since probabilities of long-term success are implied by short-term reproductive probabilities—the long-term probabilities are as it were *contained in* the short-term probabilities—we can define fitness in terms of long-term probabilities, *considering them as specifying properties of short-term probability distributions*. My illustration used discrete generations, but there are continuous-time models of similar phenomena, and short-term probabilities would also plausibly imply long-term probabilities in the more complex mathematical processes actually instantiated in nature. Thus Brandon's problem is solved. We don't have to worry that long-term probabilities don't seem to be able to be involved in causing evolution, and we might have a single way of characterizing fitness.

Moreover, to the extent that fitness should reflect probabilities of long-term success, this

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[5]For the present I assume that one-generation transition probabilities are the same in each generation, because the environment is not changing, there is no frequency-dependence, etc. Section 5 relaxes this assumption.

[6]See for example (Ewens, 2004; Grimmett and Stirzacker, 1992; Bharucha-Reid, 1960).

perspective allows a general characterization of fitness regardless of how context determines the relevant long-term probabilities: *Fitness consists of whatever mathematical properties of short-term probabilities imply probable long-term success.* Fitness can be defined in terms of long-term probabilities without losing short-term efficaciousness. In a slogan, fitness is:

Defined globally, but acts locally.

That is, fitness is defined in terms of probable long-term ("global") effects, but accomplishes them via short-term ("local") effects—whose probabilities have the properties which constitute fitness. We can call this *long-term/short-term* (LT/ST) fitness.

But how long is long enough? Surely not always Thoday's 10^8 years. (What if the entire population goes extinct before that time? All fitnesses would have been zero, and no natural selection could have taken place.)

4   Interval-relative LT/ST fitness

Natural selection is supposed to cause (or at least explain) evolution, and fitness differences are supposed to be an essential part of that cause. However, evolution over different intervals of time should be seen as different evolutionary explananda, or more precisely as different effects which might be caused by natural selection. That is, we should recognize that in different situations, we are interested in questions about different effects—about evolution over different intervals of time. But different causes may have different effects, and different explananda can have different explanantia. Thus there is no reason to expect that fitness could be defined without reference to an interval of time, and from the present perspective it makes no sense to do so. We should talk of fitness relative to an interval of time I beginning from a specified point in time t when a population is in a specified state. I'll use the terms "I-fitness", "I-fitter", etc. for fitness understood as relativized to an interval I in this way.

In keeping with the arguments for long-term/short-term fitness, I suggest that fitness be understood this way:

> A type A is I-fitter than a type B if A has a greater probability of having increased its frequency more (as a percentage of the frequency at t) than B at the end of interval I which begins at t.

For example, A might be likely to increase its frequency over a long period of time I_1, but then exhaust a resource it needs and thus go extinct before the end of I_2. In such a case A might be I_1-fitter than B but I_2-less fit than B. (Note that this definition of "fitter than" is consistent with an I-fitter type losing in a race against an I- less fit type over the interval I; fitness differences in the present sense summarize facts about probabilistic outcomes and should not be taken to guarantee any particular outcome.)

5 Short-term probabilities of what?

I argued above that we can understand fitness in terms of mathematical properties of probability distributions over numbers of offspring, even though those properties have implications for evolution many generations hence. Ariew and Lewontin (2004), and Krimbas (2004) gave a set of arguments that challenge even this possibility. These authors argued that different short-term fitness measures are needed for various cases: sexual reproduction, niche construction, overlapping generations, etc. Some of the Ariew/Lewontin/Krimbas arguments seem to show that in some contexts fitness cannot be defined by a probability distribution over offspring, or over grandoffspring, but rather distributions over many generations may be needed to define fitness. What then are we to say about Brandon's point that natural selection has to act over the short term? I'll consider some of the toughest cases raised by Ariew and Lewontin and Krimbas, arguing that taking the relevant probabilities to be of events in organisms' lives rather than of numbers of descendants plausibly allows these cases

to be handled by a sense of interval-relative fitness which is defined by short-term probabilities. More detailed descriptions of these and other interesting cases can be found in (Ariew and Lewontin, 2004; Krimbas, 2004).

Case 1: In a species with sexual reproduction, probabilities of numbers of grandoffspring will depend on offspring's mates as well parents' number of offspring. Probabilities over numbers of offspring thus don't imply long-term probabilities; probabilities over number of grandoffspring seem needed for this case. (This is so whether or not there is non-random mating.) However, probabilities of an offspring mating with organisms of various types depends on each parent's (short-term) probabilities of producing numbers of organisms *of various types* along with the distribution of parent types in the population (and other probabilities concerning mating preferences, where mating is non-random). For it is these factors which determine probabilities of different frequencies of types in the generation in which offspring mate. So probabilities of numbers of grandoffspring are implied by short-term probabilities, although over a richer space of outcomes (offspring types must be distinguished) than considered earlier. Arguments like those given in Section 3 can then show that these short-term probabilities imply long-term probabilities. Mathematical properties of the short-term probabilities are defined by these long-term probabilities, and thus can constitute LT/ST interval-relative fitness in terms of these properties. (Other cases such as frequency-dependence due to epistatic interactions between loci can be handled in a similar manner.)

Case 2: Traits affecting parental investment, parent-provided developmental context, and niche construction can indirectly affect probabilities of numbers of grandoffspring or later descendants without affecting probabilities of numbers of offspring. Such cases thus seem to require the basic "short-term" probabilities to be over numbers of grandoffspring or later descendants—potentially dozens of generations later. However, a parent's type plausibly gives rise to a probability distribution over many possible events in its life (given the makeup of its population and its environment). These probabilities include *inter alia*

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probabilities of numbers of offspring of various types, in various locations, etc., as well as probabilities of offspring-aid events, niche construction activities, etc. This variety of short-term probability (over a rich outcome space) thus implies probabilities of numbers of offspring in future generations *via* effects produced by a current organism. Again it can be argued that properties of such short-term distributions imply probabilities of long-term success, and should thus constitute a long-term/short-term fitness relative to a given interval.

Case 3: Ariew and Lewontin (2004) point out that when generations overlap, probabilities of long-term success can depend on whether the population size is increasing or decreasing. Thus it seems that fitness cannot be defined except by reference to what the population size is actually doing. Moreover, given that population changes are probabilistic, the way in which a population size changes might not be determined by facts at a given time. Ariew and Lewontin seem to suggest that in such cases fitness cannot be defined by short-term probabilities, but instead must be derived from actual events over a relatively long period of time. But this is incorrect. Probabilities of size change are implied by probabilities of events in organisms' lives such as those considered so far. (This can easily be seen from the simple 5-organism population example in §3.) Moreover, mathematics of transition probabilities for overlapping generations are well-known. Again probabilities of various multi-generation evolutionary paths of the populations would be determined by strictly short-term probabilities, so long-term/short-term fitnesses would again exist.

It thus seems plausible that interval-relative long-term/short-term fitness can be defined in terms of probable outcomes at the end of an interval I, where the long-term probabilities are implied by short-term probabilities of events in organisms' lives in various generations. The short-term transition probability distributions at various times need not be the same, but later short-term distributions will be implied by earlier short-term distributions along with initial conditions at the beginning of I. For it is the organisms at a given time which create conditions for the population a short time later by interacting with the environment

and producing offspring. (None of this need be true when environmental change is caused by factors beyond of the population in question, but that is no strike against the present view, since it's generally agreed that fitness should be sensitive to such environmental changes.)

6   Conclusion

6.1   Comparative fitness

The view which results from the preceding remarks can be be summarized as follows:

- A type A is I-fitter that B if A has a greater probability of having increased its frequency more than B at the end of the interval I, where the relevant long-term probabilities are implied by short-term, 1-generation probabilities over certain events in organisms' lives.

- The relevant interval for I-fitness is the interval over which a chosen evolutionary effect takes place.

- That fitness is constituted by short-term probabilities means that it concerns events which act over the short-term.

- Fitness is measurable in principle, but estimated in practice. Models and sampling techniques for *aspects* of preceding exist.

This provides a unified characterization of what it is for one type to be fitter than another. For a given population, there is, of course, a different fitness property for each interval I, but it should be clear now that this is what we should expect for different evolutionary effects/explananda. The present view differs from the earlier views discussed above (Brandon, 1990; Sober, 2001; Ariew and Lewontin, 2004; Krimbas, 2004) which, in various ways, allowed fitness properties to be disparate and without systematic relation to each other. Note that if the relevant short-term probabilities are causal (as they would be if they were propensities),

the present approach can help support a view of natural selection as a single kind of cause of evolution.

I want to suggest one possible further development of this view. First, notice that what makes the overlapping generations case different from those considered earlier that it requires a probability distribution over times at which a parent produces offspring. More generally, sequencing and timing of events in relation to changes of states of the environment can matter to probabilities of future proliferation. Second, I suggest, but will not argue here, that an environment should be viewed as defining a probability distribution over conditions that members of a given population might experience during the interval of time I over which fitness is to be calculated. This is to treat an environment as the environment for an entire population rather than for a specific organism.[7] These considerations suggest that the basic short-term probabilities which constitute fitness should be probabilities of sets of sequences of possible events—both organismic and environmental—in the life of an organism of a given type. We can call these sequences of events "organism-environment histories".

6.2 Population dynamics

The definition of "fitter than" given above does not resolve all what-function questions about fitness. Although the definition can be used to define a sense of comparative fitness over very short intervals I, understanding short-term dynamics usually calls for a fitness degree property. Measures of relative strength of fitnesses are also relevant to some questions about long-term evolution; we may, for example, want to know not only which type will probably go to fixation, but also how fast it is likely to do so.

In such cases the condition to be caused, explained, or predicted is more precise than the question of which type will probably increase its frequency more, etc., and the relevant notion

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[7]See (Abrams, 2007b) for a characterization of environments which is broadly consistent with the present view of fitness.

of fitness should reflect that fact. We shouldn't expect, however, that there is one scalar fitness property which can be taken to be *the* property which objectively drives all short-term dynamics. For what really drives short-term dynamics is the set of full moment-to-moment transition probability distributions for members of a population, rather than sequences of summary statistics such as expectations. The full set of transition probability distributions imply a probability distribution over all possible sequences of frequency and population size changes over an interval of time. Then we have to decide what kind of summary property of the latter distribution is of interest to us. Scalar time-indexed fitness properties can be relevant to prediction/explanation/causation of dynamics, but only relative to a precise specification of what is to be predicted/explained/etc. Thus, for example, the common use of expected number of offspring to model short-term dynamics is in fact ideal for answering one particular question: What is the the path of the average population state through the space of possible relative frequencies of types? However, that is only one of many simple questions one might ask about population dynamics.

These last remarks might make one conclude that the notion of fitness is far less unified than is suggested by the rest of the paper. Such a conclusion seems premature. For my remarks suggest only that, as in the rest of the paper, a causal and explanatory property going by the name of "fitness" must be relative to the effect to be caused or explained. I've explained how to provide a systematic characterization of comparative fitness relativized to intervals of time. There is at present no reason to think that the tools developed for that purpose cannot be used as the basis of a systematic characterization of fitness for a broader range of evolutionary effects.

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