Block Fitness

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Abstract

There are three related criteria that a concept of fitness should be able to meet: it should render the principle of natural selection non-tautologous and it should be explanatory and predictive. I argue that for fitness to be able to fulfill these criteria, it cannot be a property that changes over the course of an individual's life. Rather, I introduce a fitness concept—*Block Fitness*—and argue that an individual's genes and environment fix its fitness in such a way that each individual's fitness has a fixed value over its lifetime.
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1. Introduction

Nothing seems less controversial than the fact that the fitness of organisms changes over time. If an organism becomes ill, infertile, or otherwise compromises its chances at reproduction, its fitness will decrease. Similarly, the birth of an organism's offspring increases its fitness. Fitness also seems to fluctuate through interactions between individuals. An altruistic interaction, for example, is characterized as one involving such a change of fitness: Sober & Wilson (1998, p. 17) hold that 'A behavior is altruistic when it increases the fitness of others and decreases the fitness of the actor'.

In this paper I argue that—contrary to our intuitions—fitness *cannot* fluctuate with time: conceiving of fitness as fluctuating is problematic because such a fitness concept does not do a good job explaining and predicting evolutionary and ecological phenomena and cannot play a central role in the principle of natural selection. The fitness concept I argue

for—*Block Fitness*—is a block property, constant over an individual's lifetime, implying that no events in an individual's life, altruistic or otherwise, can change its fitness. Fitness, then, is not a function of the *actual* life that an organism lives. Rather, I will argue, it is a function of all of the *possible* lives that the organism could have lived. Although this sounds epistemologically problematic—discovering the fitness of individual organisms might seem impossible—we will see below that this conception poses no such difficulties.

This time-invariant fitness concept is in opposition to recent arguments for a Fisherian (that is, realized) conception of fitness (for example, Matthen & Ariew, 2002; Walsh, Lewens, & Ariew, 2002). Below, in arguing for Block Fitness and against realized fitness, I show that realized fitness renders the theory of natural selection tautologous. Moreover, realized fitness is not explanatory of evolutionary change.[1]

Additionally, the fitness concept argued for here implies that an individual does not simultaneously have more than one real fitness. This is in opposition to some recent pluralistic treatments of the concept of fitness. Walsh, Lewens, & Ariew (2002, p. 467), for example, argue that '[t]here may be no single correct way to calculate trait fitnesses; often enough it is simply a matter of our explanatory project'.

Although previous conceptions of fitness have not explicitly treated fitness as time-invariant, at least one of these conceptions is amenable to being time-invariant, namely the propensity interpretation of fitness (Brandon, 1978; Mills & Beatty, 1979).[2] Although a full defense of the propensity interpretation of fitness is beyond the scope of this paper, I will give partial arguments in favor of it and show how it can fill the requirement of time-invariance.

I will begin by arguing against the Fisherian conception as an adequate notion of fitness. I then argue for the constancy of fitness over an organism's lifetime. In order to do this, I introduce the notion of the fitness environment.

2. Fitness as actualization

The most straightforward conception of offspring-based fitness is the following: fitness is the number of offspring an individual[3] produces over its lifetime. This type of fitness, called realized fitness or Fisherian fitness,[4] is generally conceived of in either of two ways, *Ratchet Fitness* or *Aristotelian Fitness* (Figure 1a,b). With Ratchet Fitness, each organism

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[1] Matthen (personal commentary) feels that predictive fitness can be understood as time-invariant. Although it might be possible to interpret predictive fitness in such a way that it is time-invariant, the way in which Matthen & Ariew (2002, p. 56) describe predictive fitness—as being based on 'a statistical measure of evolutionary change . . .'—implies that predictive fitness does vary with time: because the rate of evolutionary change can fluctuate over a relatively short time scale, predictive fitness (which is based on this change) would reflect such a fluctuation.

[2] Propensities can be understood as time-invariant or as changing with time. Thus a propensity interpretation of fitness is not automatically a version of Block Fitness. However, I hold that *if* the propensities in a propensity interpretation of fitness are taken to be time-invariant, then it is compatible with Block Fitness.

[3] In the literature, realized fitness is often cast in terms of *average fitness*—the average contributions of an ensemble of individuals (organisms, alleles, etc.), not a single individual. For example, Futuyma (1986, p. 552) defines fitness as 'The average contribution of one allele or genotype to the next generation or to succeeding generations, compared with that of other alleles and genotypes'. For the purposes of this argument, the distinction between realized fitness conceived as either the contribution of one individual or as the average contribution of many is immaterial. Both fail as adequate conceptions of fitness for the same reasons.

[4] The "predictive fitness" of Matthen & Ariew (2002) is also a variety of realized fitness. It is a prospective fitness that is based on the actual (realized) evolutionary change. Because evolutionary change is a property of ensembles, not individuals, predictive fitness is a property of ensembles, not individuals.
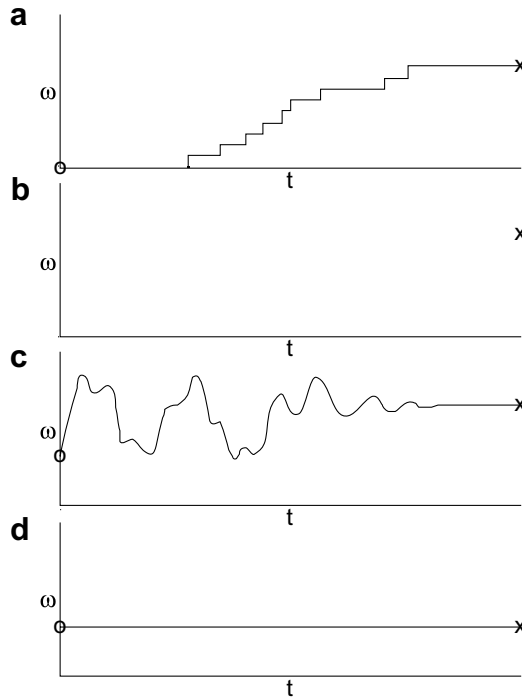
Fig. 1. a. Ratchet Fitness; b. Aristotelian Fitness; c. Flux Fitness; d. Block Fitness. ω = fitness; t = time; 'o' denotes birth; '×' denotes death.

is born with zero fitness and its fitness is ratcheted up with each successful act of reproduction. With Aristotelian Fitness, on the other hand, an organism has a determinate fitness only upon death. Upon death, its fitness is the number of its descendents. There is a great epistemological benefit to these conceptions. One can observe a population of organisms through their lives and determine, absolutely, the fitness of each. Despite this benefit, the problems with realized fitness[5] are many.

First, realized fitness allows stochastic factors to modify an individual's fitness. If one of two identical[6] organisms is struck by lightning and killed but the other goes on to have three offspring, they will, under this conception, have different fitnesses. But this fitness difference is not due to the constitution of the organism. Rather, it is solely due to a stochastic environmental factor. This is problematic since fitness, it seems, should be identical for identical individuals in the same environment. This modification of fitness by chance occurrences in organisms' lives is the central problem with this concept of fitness, and the second and third problems are a consequence of this problem.

Second, realized fitness is not explanatory. One desideratum of the concept of fitness is that the fitness of an organism (or organism type) can be invoked to explain why it had more or fewer offspring than one of its conspecifics (or an alternate conspecific type).

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[5] I will use "realized fitness" to refer generically to Ratchet Fitness and Aristotelian Fitness.
[6] Identical in all properties save spatial position. There of course cannot be two organisms identical in all properties.

But if fitness *is* the number of offspring actually produced, then it cannot *explain* the number of offspring actually produced. This is the notorious "tautology problem" or "explanatory circle" that has convinced some that the theory of natural selection is empirically empty, a mere tautology.

Third, realized fitness is not a good predictor.[7] If an organism dies with a fitness of six (offspring) this fact does not accurately predict how many offspring another organism of the same kind will (or is likely to) bear. The organism might have gotten "lucky" and produced many more offspring than others of the same type will (or are likely to) bear. This is analogous to the fact that the outcome of one roll of a die does not predict the outcome of rolling other dice of the same type. Rolling a "three" might carry the information that it is possible to roll a three. But it does not tell you the crucial information, for example, that there is a 1/6 chance of rolling a three or that there are six possible outcomes. To predict the outcome of the die, we need information about the die, such as the fact that it has six faces each with an equal probability of landing face-up, that one face of the die has one pip, another has two, and so on. This information is absent from the concept of realized fitness.

Given these three problems, it seems that we need a different concept of fitness. Does this mean that realized fitness is of no use? No. Realized fitness is very important for ecology and evolutionary biology. Realized fitness is a *measure* of the theoretically adequate conception of fitness. But realized fitness should not be confused with the fitness concept that is central to the theory of natural selection.

3. Fitness as lifetime propensity

The propensity interpretation of fitness as expressed by Brandon (1978) and Mills & Beatty (1979) purports to break the explanatory circle by conceiving of fitness as a propensity to produce offspring.[8] The circle is broken since the actual number of offspring an organism produces need not equal its propensity to produce offspring. The propensity to produce some number of offspring is like the propensity gold has for dissolving in mercury. If some ingot of gold never happens to contact, and thus dissolve in, a pool of mercury, this does nothing to weaken our claim that it has this propensity. It is a version of this account of fitness that will be argued for below. Fitness, I will argue, is best conceived as a function[9] of the probability distribution of all the possible numbers of offspring the

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[7] An average realized fitness, however, can be a good predictor.

[8] "Offspring" can refer to offspring of genes, organisms, groups, etc. The view presented here is neutral with respect to these entities, that is, it is not making a claim in the levels of selection debate. It is a further question (and not one that I will address here) which entities should be thought of as having a fitness. In what follows I will, for the sake of simplicity, refer only to organisms. This should not be taken as an assumption that organisms are the only kind of entity that can properly be said to have a fitness. Rather, "organism" should be read as a placeholder for whatever entity that can properly be said to have a fitness.

[9] Specifying what, precisely, this function is is not a trivial task. The original formulation of Brandon (1978) was inadequate because it did not incorporate variance in the distribution of possible numbers of offspring produced. See Brandon (1990) for a revised version. For a discussion of some of the difficulties with the propensity interpretation of fitness see Beatty & Finsen (1989) and Sober (2001). It is beyond the scope of this paper to attempt to specify what, exactly, this function is. Even if one feels that the latest versions of the propensity interpretation of fitness are problematic, and that this is reason for thinking that fitness cannot be understood in terms of a propensity, my arguments for an unchanging fitness still hold: for fitness to be explanatory and play a role in the theory of natural selection, it cannot fluctuate over the course of an organism's lifetime.
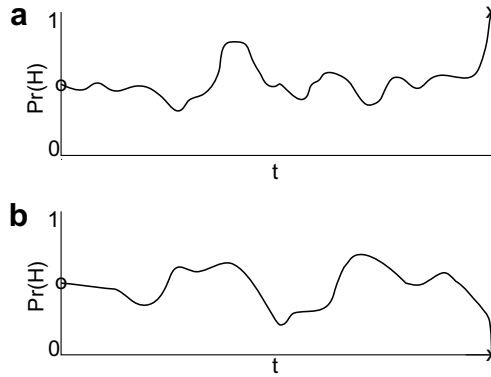
Fig. 2. a. The coin lands heads-up; b. The coin lands tails-up. 'Pr(H)' denotes the probability of landing heads-up; t = time; 'o' denotes birth; '×' denotes death.

individual might produce. Including the indirect component of fitness, the full characterization is this: fitness is some function of (1) the probability distribution of all the possible numbers of offspring the individual might produce plus (2) the probability distributions of all the possible numbers of offspring all of the individual's relatives might produce multiplied by their degree of relatedness to the individual. It is standard to refer to (1) as direct fitness, (2) as indirect fitness, and the sum of (1) and (2) as inclusive fitness. In what follows, I will, for the sake of simplicity, speak of fitness as being about the number of offspring produced. But it should be understood as implicit that it is inclusive, not direct, fitness that is being discussed.

There are two chief ways in which fitness as a propensity might be conceptualized, what I will call *Flux Fitness* and *Block Fitness* (Figure 1c,d). With Flux Fitness, the fitness of an organism at time t is a function of the number of offspring it is expected to produce based on its circumstances at time t. Since an organism's circumstances are always changing, its fitness is in flux. But as an organism approaches the end of its life, its possibilities of engendering more offspring are reduced. As this occurs, its fitness is damped. When it can no longer have any more offspring, its fitness becomes fixed.[10]

Many of the problems with realized fitness also plague Flux Fitness. To see why this is the case, and to see why Block Fitness is immune to these problems, let's turn to an analogy. Consider a coin flipping device in a box. The box is perforated by dozens of small holes and air is blown in and out of the holes. The air is sufficiently strong as to change the outcome of a coin flip. Furthermore, the air is blown in and out of the holes in a random[11] fashion. Thus, the outcome of each flip of the coin is random. If we plot the probability that a given coin will land heads-up given its current situation, we might get a graph like that of Figure 2a. Figure 2a corresponds to the Flux Fitness graph in Figure 1c: at each time t, the probability of landing heads-up is based in its circumstances at time t. The coin represented in Figure 2a happened to land heads-up.

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[10] Actually, because of indirect fitness effects, it is possible to have post-infertility fitness fluctuations. An organism can, for example, devote itself to caring for its still-reproducing siblings.

[11] Random, here, meaning uncorrelated with states of the coin. The addition of air is meant to free the outcome from the inherent biases of coin flipping machines (see Diaconis, 2004).

Given the outcome of the coin flip in Figure 2a (heads), or the instantaneous probability some time prior to landing heads, are we able to predict the outcome of another flip of the same coin or a flip of a different coin of the same type? That the coin happened to land heads-up merely tells us that heads is a possible outcome of flipping a coin of this type. It does not tell us that it is rare or common. And it certainly does not tell us what we want to know, that is, that coins of this type have a probability of 0.5 of landing heads. We want to know the probability of landing heads in this environment for this type of coin. The instantaneous probability of a coin during its flip gives us no such information. Thus, the instantaneous probabilities represented in Figure 2a are not very predictive. Likewise, Flux Fitness is not very predictive. Knowing that a four-year-old organism has a probability of 0.7 of producing four offspring does not enable us to predict that another organism of the same type is likely to have four offspring. All we learn is that four is a possible number of offspring for individuals of that type, and that for this particular individual at this point in its life it has a high probability of having this number of offspring. It could be the case that the most likely number of offspring for individuals of this type is two. That Flux Fitness is not very predictive should be no surprise, since Flux Fitness and realized fitness converge as the individuals approach death (that is, as t approaches $\times$).

Running identical coins through the coin flipping box will give different curves. If we were to flip another coin in the same box, its curve might be something like 2b (in which the coin lands tails-up). Thus, identical coins can precipitate very different probability curves. The difference in curves is not explained by differences in the coins, since there are no such differences. Instead, the differences are due to random variations in the environment, which shows that random factors are incorporated into the probability curves. Likewise, the fitness curve for Flux Fitness is contingent upon random occurrences in the organism's past.

How might we remedy this conception of fitness? With the coin example, what would be ideal for predicting the outcome of a toss of the coin? We do not want to know what the instantaneous probability of the coin is during its flip. Rather, we want to know this: given this coin and this box, what is the probability that the coin will land heads-up? The answer, assuming it is a fair coin, is 0.5. It is this probability that we could use in predicting the outcome of coins of the same type. This probability is given by the constitution of the box and the coin. It is thus fixed and does not fluctuate with time. The fitness analogue is Block Fitness. Block Fitness is based on the environment and genes of the individual and does not fluctuate with time. This drives a wedge between random ''lucky'' or ''unlucky'' events that happen to occur during its life, and its fitness. By purging individual random events from an individual's fitness, ''survival of the fittest'' becomes meaningful. An individual, or type of individual, can survive and out-reproduce another because it is more fit, that is, because it has a higher probability of having more offspring.

4. Objections

It might be objected that Block Fitness couldn't be right, since organisms can clearly alter their fitness. In the case of humans, a possible (rather extreme) example of increasing one's fitness would be a male who decided to donate to as many sperm banks as possible, thereby greatly enhancing his genetic representation in the next generation. Has he thereby increased his fitness? He has not. The reason is that the probability distribution for the

sperm donor (and, perhaps, others in the population) includes the unlikely possibility that the individual will be enamored of the idea of donating sperm and donate as much as possible. One might have in their probability distribution a $\mathrm{Pr}(100 \text{ offspring}) = 1 \times 10^{-8}$. Visiting the sperm banks and thereby having 100 offspring may be incredibly unlikely, but exhibiting this behavior and obtaining this outcome does not alter the probability distribution. Analogously, rolling a six each time in ten rolls of a die is an unlikely event, but it does not prove that the die is biased. And even if the die is biased, for example, if the probability of rolling a 6 is other than 1/6, the rolling of the die does not *engender* the bias. The bias preexists the rolling of the die.

Although one might concede that an organism cannot alter its own fitness, it might still be objected that it is nonetheless possible to raise or lower an organism's fitness through, for example, experimental manipulation. Basolo (1990, 1995) attempted to establish the fact that in the fish family Poeciliidae the female preference for males with caudal swords preceded the evolution of swordtails from their swordless ancestors. One of the key experiments involved attaching artificial swords to swordless congeners (platyfish in the genus *Xiphophorus*) and observing whether female platyfish prefer males with swords. She found that female platyfish do indeed prefer males with swords. From this, it might seem reasonable to infer that if one took a male platyfish from a wild population, surgically attached a sword, then released it into its original population, its fitness would thereby have increased (assuming, of course, that the artificial sword does not significantly increase the probability of predation or disease). But this inference is not warranted. If the researcher drew the male at random from all of the males in the population, then the acquisition of a sword is random with respect to the traits of individual males. Each of the males is equally likely to acquire a sword. Thus, receiving a sword is just a matter of good luck, not explainable by reference to specific traits or dispositions.

But there is another possibility. Perhaps the researcher does not just attach swords to random males, but instead selects males of a certain kind, that is, males with a non-universal trait. Let's say the researcher attaches swords only to males that are in the top 10% with respect to body size. Furthermore, let's assume that the researcher does this generation after generation. Assuming there is a genetic basis for body size differences, there will be a response to this selection: average body size will increase. How should we interpret this situation? Consistent with Block Fitness, this scenario would thus be described: the platyfish that have the greatest probability of having a body size in the top 10% will thereby have higher fitness than conspecifics with a lower probability, other things being equal. The fact that some particular platyfish happens to have a sword added by a researcher does not thereby raise its fitness.

A third objection that could be raised is that the coin in the box is not properly analogous to organisms because the coin remains morphologically unchanged throughout its life whereas organisms undergo radical change. To see that this is not a problem, we can add morphological change to the coin. Imagine that not just air, but also droplets of molten metal stream in through the holes in the box. During the coin's trajectory it accretes, changing its physical characteristics. Because of this accretion, the probability that a coin will land tails-up might reach zero. This is analogous to an organism becoming sterilized prior to reproduction and having its chance of reproducing reach zero. Does this show that fitness can become zero during an organism's lifetime? No, just as the probability of the coin landing on a particular side is 0.5 in this molten metal bombarded box, so too the fitness of an organism does not change. It may have more or fewer offspring

depending upon how it happens to encounter the fine-grained heterogeneity (Levins, 1964) of its environment. But this randomness is not fitness-affecting.

A fourth objection is that it is unwarranted to claim that the environment in which one coin is flipped is the same environment in which another coin is flipped. Perhaps each coin is flipped in a unique environment. Likewise, each individual organism might be thought to live in its own unique environment. And since fitness is a function of environment and genes, identical coins or organisms can have different fitnesses. To answer this objection, a discussion of the concept of environment is necessary. The answer to this objection will be addressed in the following section.

5. Fitness and the environment

If fitness is Block Fitness, what fixes fitness? The short answer is that an organism's fitness is fixed by its genes and environment. It is more or less clear what "genes" is referring to,[12] but what is an environment? Consider these two statements:

(1) An organism's genes and environment fix its fitness.
(2) Fitness is a relational property between organisms of the same species in the same environment.

There is one sense of the term "environment" that I will call an *individual environment*. An individual environment comprises all of the environmental influences that happen to impinge upon an organism during its life, that is, everything an individual encounters in its space-time trajectory. An organism's development is a function of its individual environment and its genes. But is an individual environment the environment referred to in (1) and (2)? It is obvious that the environment referred to in (2) cannot be an individual environment because, since each individual environment is unique, there is no sense in which different organisms can occupy the "same" individual environment. And since "environment" in (1) and (2) need to co-refer, a different concept of environment is needed. Why does "environment" in (1) and (2) need to co-refer? If it did not, "fitness" would refer to a different property in (1) and (2). But in order to have a theoretically unified concept of fitness that we can use to compare different individuals, "fitness" in (1) and (2) must be co-referential.

What concept of environment will accord with both (1) and (2)? It must be an environment that is expanded beyond an individual environment. But how far this environment is to be expanded and what constitute its limits is difficult to discern. One contender for an expanded concept of environment is a *species environment*. A species environment comprises all of the environmental influences that impinge upon all of the individuals of a species during their lives. Although attractive, for many species a species environment is far too broad to fit our criteria. If we are asking, for example, which of two Virginia opossums

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[12] Although it might be relatively clear what we mean by "gene", it is not clear that genes should be thought to exhaust the important hereditary material. In sexually-reproducing organisms, not only are genes inherited from the parents, cytoplasmic material is inherited from the mother. If there are significant differences in cytological material among individuals in a population, these differences might be fitness-affecting. But if the population lacks significant cytoplasmic heterogeneity, or if the heterogeneity makes little difference in the cell's functioning, then the cytoplasm can be ignored. Henceforth, "gene" should be read as a placeholder for "the hereditary material that constitutes significant differences between individuals".

living in a suburb of Memphis, Tennessee is the fittest, facts about a rainforest in Brazil, where members of the species also reside, should not bear on the calculation. The suburban opossums are in no significant way causally interacting with individuals in the rainforest in Brazil; it makes no difference to them whether or not individuals in the rainforest exists. It may be the case that some of the genes from the suburban opossums might eventually make it south to Brazil, but if this were to occur, it would likely take centuries. And since what may occur centuries later has no bearing on how well these opossums are currently surviving and reproducing, this long-term gene flow does not bear on their fitness.

Thus we need a concept of environment that is larger than an individual environment but smaller than a species environment (for at least some species). One possibility for such an environment is the *selective environment* (as introduced by Antonovics, Ellstrand, & Brandon, 1988, and elaborated by Brandon, 1990). Although in some cases, the selective environment would be the environment that fixes fitnesses, it is not always the case. The reason is that an individual's fitness might be fixed by more than one selective environment. Thus a concept of environment that can encompass multiple selective environments is needed. I will call this environment the *fitness environment*. The question of how this environment is delimited will be taken up in the next section.

6. Operationalization

A conception of fitness and environment that cannot be applied to the natural world—that does not predict or explain the fates of biological entities—is of little use. Because of this I will now turn to the question of how Block Fitness can be operationalized.

Block Fitness, as mentioned above, is not based on the actual life that an individual lives. It is based instead on all of the possible lives—possible paths through space and time—it could have lived. Some of these paths would include contracting a disease or being killed while young, while other paths will be long and include numerous instances of successful reproduction. Which path is realized is a matter of chance, but features of the paths make some reproductive outcomes more likely than others. For example, consider some component of fitness, leaf waxiness. We might examine plants in a xeric environment and observe that individuals with one allele always have very waxy leaves while the individuals with an alternate allele have less waxy leaves. These components of fitness add up to make one variant fitter than another in the following way: the waxy variant will be fitter if the number of successful reproductive events in the sum of its possible lives is greater, or the variance smaller, than for the less waxy variant.

Given that Block Fitness is based on all of the possible life-paths an individual might realize, it would seem impossible to measure an individual's fitness. To know the fitness of an individual, one might object, we would have to know all of the infinite number of ways it might live its life. But since this is unknowable, an individual's fitness is unknowable. To see why this objection is not a problem, we could make the analogous objection about the coin: the probability that a coin will land heads in the box is not knowable since there are an infinite number of paths the coin might take through the box. But this objection cuts no ice since we *can* know what the probability of landing heads is for the coin. One way to learn this is by examining the coin and the box and observing that the coin is symmetrical, that the box has no way of recognizing and acting differentially with respect to either side of the coin, etc. From these data we can say with some confidence that the probability of the coin landing heads is 0.5. Another way to get at this information is to

flip the coin multiple times (or flip multiple coins of the same type) and see what trend emerges. These two methods can be combined for more assurance. We can do the same thing with organisms. We might examine the plants in the xeric environment and reason that the cost of building the wax is less than the benefit accrued from decreased water loss. We could then judge that the waxy individuals are fitter than the less waxy individuals. In addition, we could conduct field observations and see whether individuals of one kind tend to have more offspring than the other kind. We need not consider every possible life a plant might live. We just need a general understanding of the sum of these lives. Similarly, we need not map out all of the possible paths a coin might travel through the box. We merely need to know that the sum of the paths that end heads-up equals the sum that ends tails-up.

As was evinced by the previous section, the concept of environment is central to the concept of fitness. Fitness comparisons are only properly made between individuals in the same environment. But what delimits such an environment and how can it be determined whether two individuals occupy the same environment? I suggest that organisms carve out their fitness environment in the following way: an organism O's fitness environment is the subset of its species environment that is likely to affect O, all of O's possible mates, all of O's possible offspring, all of O's possible grandoffspring, etc. How do we fill out the "etcetera", that is, how many generations later are counted? This is not a question that can be answered in the abstract. Rather, the number of generations depends on a variety of factors including O and O's possible mates' traits, genetic constitution, and ecological setting. For example, at one extreme might be a species in a very homogeneous environment that lacks fertility-compromising mutations, in which one generation might suffice. At the other extreme are cases of progressive telomere shortening mortal germline mutants that can take more than a dozen generations for sterile phenotypes to occur (see Ahmed & Hodgkin, 2000). Since biologists often want to obtain estimates of fitness from field observations, they need to know how many generations ahead to look in estimating fitness. Because this is an important point, I will illustrate some of the ways in which the number of generations is determined.

One condition for O's fitness environment is that O and O's descendents[13] have a high probability of *covering* the fitness environment. What does it mean to *cover* an environment? For O to cover an environment is for O to be affected by each environmental factor in roughly the proportion that each factor *effectively* exists in the environment. For example, consider Figure 3a. The fitness environment of O is illustrated. The shaded spots represent the presence of environmental factor f. In 3a it is apparent that O is likely to cover the environment by itself, that is, O is in the presence of f in about the proportion that f is in the fitness environment. Because of this, a good fitness estimate could be obtained for O without having to follow its progeny through many generations or observe the reproductive output of many individuals similar to O. If O had a much shorter life or moved much more slowly, however, it would be rather unlikely that it covered the fitness environment. This is represented by Figure 3b. In this case, the fitness environment is likely to be covered only by O plus O's descendents.

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[13] Actually, the full characterization is "O's descendents, relatives, and relatives' descendents". But as mentioned at the beginning of Section 3, for expositional simplicity, relatives (and their descendents) should be taken as implicit.
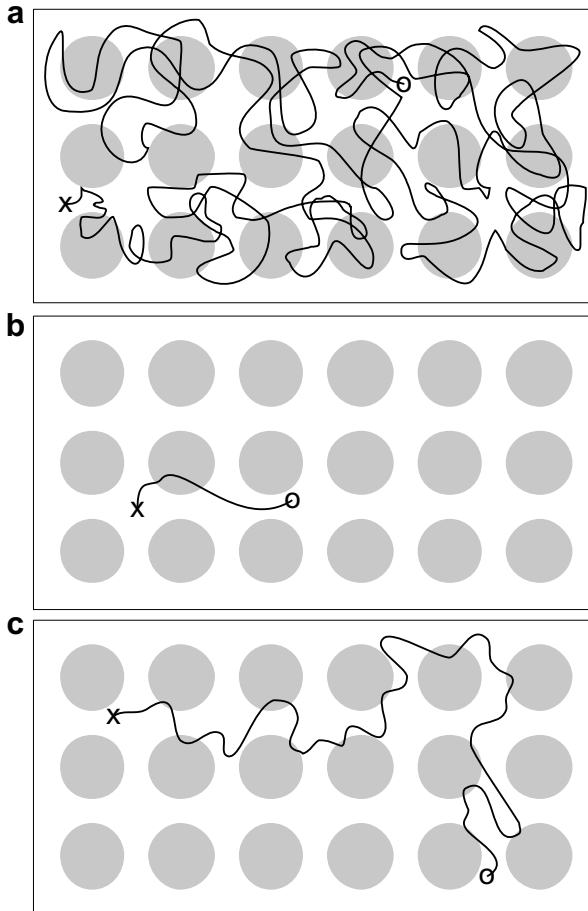
Fig. 3. 'o' denotes birth; '×' denotes death. The line connecting 'o' and '×' denotes *O*'s space-time trajectory. The shaded spots represent the presence of environmental factor *f*.

In the above description of covering an environment I referred to the proportion that each factor *effectively* exists. Why add "effectively"? In 3a and 3b *O* acted indiscriminately with respect to factor *f*. But this does not have to be the case. It could be that *O* has an aversion to *f* and that when it encounters the parts of its environment exhibiting *f*, it soon moves to an *f*-free region, as depicted in 3c. In 3c, there is a disparity between the area exhibiting *f* and the amount of time *O* is in the area exhibiting *f*. Because of *O*'s disposition, *f* effectively constitutes a much smaller part of *O*'s environment than might be assumed.

It should be noted that this understanding of organisms (plus descendents) covering the fitness environment implies that the organism (plus descendents) and environment are mutually constituting. To illustrate, the structure of the fitness environment is an effect of how many generations of descendents "count" toward creating *O*'s fitness environment. The more generations, the broader the fitness environment. But the number of generations of descendents that "count" is to a great extent determined by the environment

(a heterogeneous environment would need more iterations, a homogeneous fewer). This in no way undermines the truth of my claims. Rather, it shows that modeling such situations would be difficult. This is similar to the way in which an organism's genes and individual environment are mutually constituting: the environment controls, to some extent, which genes are expressed, but which genes are expressed determine, to some extent, the individual environment.

What other factors might determine the number of generations that one would have to consider in estimating O's fitness? If O were disposed to choose mates with ''bad'' genes, for example, individuals with a higher than average number of deleterious recessive alleles, and if O were disposed to pass this disposition on to its offspring, then several generations later traits due to these alleles might emerge. This problem does not (phenotypically) appear if one looks just one generation ahead. Clutch size in birds provides an example of the need to look more than one generation ahead: a large clutch might be most productive in producing offspring during moist years, but unsustainable during dry years. Thus, the fitness would consist in performance in both moist and dry years. Both moist and dry years would be *covered* by the descendents.

From these reflections, it might seem that the number of generations that count toward an organism's fitness is likely very many, and that this militates against its operationalization. While it is true that as the number of generations of descendents that count toward an organism's fitness increases, the probability that the fitness environment is covered increases. But there is good reason to think that these later generations do not count toward an organism's fitness. Assuming O reproduces sexually, its offspring are related[14] to it by a factor of 0.5, its grandoffspring by 0.25, its great grandoffspring by 0.125, and so on. It is quite apparent that one's descendent a dozen generations later bears little relation to it relative to other conspecifics. Also, since evolution is occurring, O's descendents many generations later may not closely resemble O. This is why one ought to reject long-term notions of fitness.[15]

It might be thought that the way I defined a fitness environment makes it no different from a species environment. Recall that an organism O's fitness environment is the subset of its species environment that is likely to affect organism O, all of O's possible mates, all of O's possible offspring, all of O's possible grandoffspring, etc. One might form this objection: if an organism's fitness is in part constituted by its possible mates and the fitness of its possible mates is in part constituted by their possible mates, then the chain of possible mates might reach every reproductively viable individual in the species. The opossums in Memphis might be in the same fitness environment as the opossums in Brazil after all.

The reason that this is not the case is the following. There are two components to O's fitness that are constituted by its possible mates, one genetic and another phenotypic. The

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[14] Related, that is, relative to random individuals in the population.

[15] A conception of fitness that consists in the fate of descendents many generations later was argued for by Thoday (1953). His concept of fitness takes into account 10^8 generations. More recently, Cooper (1984) takes fitness to be the expected time to extinction, ETE: individual x is fitter than y if y's lineage is expected to go extinct first. The main problem with these long-term approaches is that selection is not future-sighted. Selection acts on organisms as they currently are, not what might happen to their progeny thousands of generations later. Also, since evolution is taking place, each offspring is somewhat different from its parents and these differences can accrue. What goes extinct 10^8 generations from now might not even belong to the same species whose fitness we want to determine. Thus these long-term notions do not seem to be the kind of concepts that can explain current reproductive success.

genetic component travels only vertically (from parent to offspring). Let's assume that the individuals in O's group mate with multiple individuals and (at least occasionally) bear offspring from multiple mates. How well O's offspring fare is due in part to the genes that the offspring received from O's mate. And how well all of O's mates' offspring fare is in part a function of the genes O's mates' offspring received from O's mates' mates. But there is no gene flow from O's mates' mates to O's offspring, that is, there is no horizontal or oblique genetic transmission. Because this is the case, the pool of individuals that affect O's fitness via direct genetic means extends no further than O's possible mates. Thus, with this genetic component there is no possibility that the opossums in Brazil will be within the fitness environment of an opossum in Memphis.

But what about the phenotypic component? If O's fitness is in part constituted by its phenotypic interaction with its possible mates, and if the fitness of each of O's possible mates is in part constituted by its phenotypic interaction with their possible mates, than it seems that one could follow this ''possible mates'' chain until every reproductively viable individual has been included. From this it would seem to follow that individuals in Brazil and Memphis might inhabit the same fitness environment. The reason that this is not the case is that one's possible mates only *partially* constitute one's fitness. Having the possible mates that O has (relative to some other set of possible mates) is fitness altering by some fraction $1/x$. Having the possible mates that O's possible mates have (relative to some other set of possible mates) is fitness altering by some fraction $1/y$. The fractional change to O's fitness of a change in possible mates of O's possible mates is $1/xy$. A change in the next shell of possible mates would alter O's fitness by factor $1/xyz$, and so on. So as one follows the possible mate chain, the extent to which the possible mates affect O's fitness undergoes a geometric decay. Thus after a small number of links the effect essentially goes to zero.

We have seen that although an individual's fitness consists in a vast number of environmental factors, it is nonetheless possible to gain knowledge of an organism's fitness. In fact, I would argue that Block Fitness is often implicitly assumed in biology: if, for example, a *Drosophila* researcher thinks an individual fly of type A is fitter than an individual of type B in some common environment E, she will *not* take this to be disproved if a type A individual produces fewer descendents than a type B individual. Instead, she will test her hypothesis by looking at the number of offspring produced by a large number of A and B individuals in E and take the average. Although some biologists erroneously *define* fitness as this average (and thus mistake fitness for the measurement of fitness), this process assumes Block Fitness. Because of this, I hold that the operationalization of Block Fitness is not problematic, and in many cases would not prescribe biologists to make different observations or conduct different experiments (though it might prescribe a different way of talking about what they are doing).

7. Conclusions

We have seen that (1) an individual's fitness is fixed over its lifetime, that is, its fitness cannot increase or decrease with time, and (2) fitness comparisons can only occur between conspecifics that occupy the same fitness environment. What implications does this have for ecology and evolution? The view implies that *nothing* that an organism does or has done to it affects its fitness. The honeybee that attacks and stings an interloper will not thereby alter its fitness. A meerkat disposed to spend a disproportionate amount of time

on sentinel duty may thereby have a lower fitness than another that is disposed to shirk its duty. But no meerkat lowers its fitness by acting as a sentinel. Similarly, a soldier does not lower her fitness by charging forth in battle. Indeed, the soldier may have a low fitness and this low fitness may be an effect of her disposition to act selflessly, but her low fitness is not an effect of how she actually acts. Her selfless actions might be evidence for her low fitness, but they do not constitute her fitness. It could be the case that all of the individuals in battle have the same fitness, but that some act selflessly due to the fine-grained heterogeneity of their environment (Levins, 1964). Similarly, interactions between individuals do not alter fitness. What game theory shows us is *not* how individual fitness is increased or decreased through behaving in certain games in certain ways. Rather, via game theory we can learn why organism *O*, being disposed to participate in certain games in certain ways, is more or less fit than other organisms with differing dispositions.

This conception of fitness thus has a profound effect on how we should think about the consequences of particular occurrences in an individual's life. It also changes the way we ought to think about the interactions between individuals (or groups). These interactions are often characterized as being, for example, mutualistic, parasitic, commensalistic, or altruistic. And these interactions are characterized in terms of fitness *changes*. For example, an altruistic act is often said to be one in which the recipient gains (or increases in) fitness while the altruist (or donor) decreases in fitness.[16] But, as we have seen, fitness is not something capable of change. Does this mean that the above view of fitness does not allow for altruism (or mutualism or parasitism or any such relationship) to obtain? No. An altruistic act could be characterized as an act such that (1) an individual disposed to perform the act is less fit than another individual lacking this disposition and (2) an individual disposed to be a recipient of such an act is fitter than another individual lacking this disposition.

A fixed fitness also bears on the levels of selection debates. Those advocating multi-level selection often speak of "within-group fitness" and "overall fitness". The inference from individuals with trait *x* having a higher "overall" or "average" fitness than individuals lacking trait *x* (other things being equal) to the claim that *x* is promoted by individual (and not group) selection is rightly argued against by Sober & Wilson (1998). The mistake they and others make is to think that individuals have multiple fitnesses (say, one overall and another group relative). This is a mistake because *O* cannot have fitness *x* within group *G*, but have an overall fitness of *y*, where *x* ≠ *y*. The fitness fixed by *O*'s fitness environment is its unique fitness. And it is an empirical fact whether or not *O*'s fitness environment transcends *G*. If *O*'s environment does transcend *G* and includes groups *H* and *I*, does it make any sense to speak of its within-group fitness, that is, its fitness within *G*? It does, but only hypothetically. To say that *O*'s within-group fitness is *x* is to say that if *O*'s fitness environment included only individuals in *G*, its fitness would be *x*. What good is this counterfactual within-group fitness? It sheds light on the process of selection. Selection may be occurring at various levels of organization, and an organism's fitness environment may include more than one selective environment, but there is only one non-counterfactual fitness. One remedy to the within-group and overall conceptions of fitness is to speak, instead, of *components of fitness*. *O*'s being in group *G* relative to some other group *H* is in part constitutive of its fitness. This part can be described as a component of *O*'s fitness due to its residence in that group.

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[16] See the quote by Sober & Wilson (1998) in Section 1.

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References

Ahmed, S., & Hodgkin, J. (2000). MRT-2 checkpoint protein is required for germline immortality and telomere replication in C. elegans. *Nature*, *403*, 159–164.

Antonovics, J., Ellstrand, N. C., & Brandon, R. N. (1988). Environmental variation and genetic variation: Expectations and experiments. In L. D. Gottlieb, & S. K. Jain (Eds.), *Plant evolutionary biology* (pp. 275–303). New York: Chapman & Hall.

Basolo, A. L. (1990). Female preference predates the evolution of the sword in swordtail fish. *Science*, *250*, 808–810.

Basolo, A. L. (1995). Phylogenetic evidence for the role of a pre-existing bias in sexual selection. *Proceedings of the Royal Society of London B*, *259*, 307–311.

Beatty, J. H., & Finsen, S. (1989). Rethinking the propensity interpretation: A peek inside Pandora's box. In M. Ruse (Ed.), *What the philosophy of biology is* (pp. 17–30). Dordrecht: Kluwer.

Brandon, R. N. (1978). Adaptation and evolutionary theory. *Studies in History and Philosophy of Science*, *9*, 181–206.

Brandon, R. N. (1990). *Adaptation and environment*. Princeton: Princeton University Press.

Cooper, W. S. (1984). Expected time to extinction and the concept of fundamental fitness. *Journal of Theoretical Biology*, *107*, 603–629.

Diaconis, P. (2004). The search for randomness. American Association for the Advancement of Science Annual Meeting, February 14, Seattle.

Futuyma, D. (1986). *Evolutionary biology* (2nd ed.). Sunderland, MA: Sinauer.

Levins, R. (1964). *Evolution in changing environments: Some theoretical explorations*. Princeton, NJ: Princeton University Press.

Matthen, M., & Ariew, A. (2002). Two ways of thinking about fitness and natural selection. *The Journal of Philosophy*, *49*, 55–83.

Mills, S. K., & Beatty, J. H. (1979). The propensity interpretation of fitness. *Philosophy of Science*, *46*, 263–286.

Sober, E. (2001). The two faces of fitness. In R. Singh, D. Paul, & J. Beatty (Eds.), *Thinking about evolution: Historical, philosophical, and political perspectives* (pp. 309–321). Cambridge: Cambridge University Press.

Sober, E., & Wilson, D. S. (1998). *Unto others*. Cambridge, MA: Harvard University Press.

Thoday, J. M. (1953). Components of fitness. *Symposia of the Society for Experimental Biology*, *7*, 96–113.

Walsh, D. M., Lewens, T., & Ariew, A. (2002). The trials of life: Natural selection and random drift. *Philosophy of Science*, *69*, 452–473.