

Rethinking the Propensity Interpretation: A Peek Inside Pandora's Box¹

JOHN BEATTY^a and SUSAN FINSEN^b

^a *Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, MN 55455, U.S.A.*

^b *Department of Philosophy, California State University at San Bernardino, San Bernardino, CA 92407, U.S.A.*

Introduction

Over the past ten years, the propensity interpretation of fitness has attracted a number of proponents² and a few, persistent detractors.³ Here, two previous supporters turn critics, to acknowledge and reframe some old problems, and to introduce some additional difficulties. We are not sure whether a radically revised interpretation of fitness is necessary. But it does seem to us that certain gross oversimplifications of the propensity interpretation deserve more serious attention.

We most certainly do not propose to return to the interpretation of fitness that the propensity interpretation was designed to replace. Whatever fitness is, it is not actual offspring contribution, although it was long misconceived as such.⁴ The misconception had two sources. The first source was the operationalist fallacy of conflating properties with the manner in which they are measured, as if temperature, for instance, were best conceived as just the height of mercury in a glass column. Actual offspring contribution remains the most common and surest means of measuring fitness (especially considering the alternatives, like optimality models). But that does not mean that fitness is *just* offspring contribution. The second source of the misconception was the false assumption that it is a law of nature that the fittest always leave more offspring, which is too often thought to be one of Darwin's main insights, although Darwin was actually much more careful in this respect (see further). Current evolutionary theory allows differential descendant contribution to be a matter of chance as well as a matter of fitness, to the extent that, in small enough populations, the fitter type can leave less descendants on average, and dwindle in frequency relative to the less fit type.

The conception of fitness as mere offspring contribution has by now received so much criticism that its difficulties do not merit any further discussion here. The most common substitute, the propensity interpretation of fitness, also requires only a brief introduction. Part and parcel of the propensity interpretation is the notion that fitter organisms have greater *ability* to leave offspring, and not just (and not even necessarily) greater *success* in that regard. The propensity interpretation thus avoids the operationalist fallacy by identifying fitness with offspring contribution

M. Ruse (editor), What the Philosophy of Biology is. pp. 17–30.

© 1989 Kluwer Academic Publishers, Dordrecht – Printed in the Netherlands.

ability rather than with some record of that ability. The other important aspect of the propensity interpretation is the notion that fitter organisms only *probably* leave more offspring than the lesser fit. Darwin himself always wrote of those organisms whose particular abilities gave them 'the best chance' of surviving and reproducing (e.g., Darwin 1859, pp. 61, 81). Fitness, then, is probable offspring contribution, where the probable contribution of an organism depends on its abilities to survive and reproduce in the environment it inhabits. Organisms whose properties confer on them the same offspring contribution abilities in an environment may, by chance, leave different numbers of offspring.

Viable alternatives

But the propensity interpretation leaves much to be desired. In the first place, it is all too often paraded as *the* propensity/probabilistic alternative to the more deterministic and operationalistic conception of fitness. In the course of this paper, we will discuss a number of more subtle variants on 'the' propensity interpretation as it is usually elaborated. There are also a couple more radical variants worth pointing out. One is Thoday's (1953) notion of fitness as probability of representation over a given period of time. Another is Cooper's (1984) notion of fitness as probable duration of representation, or, in Cooper's own terms, 'expected time to extinction' (ETE). These two interpretations, and the rationales behind them, are somewhat similar. We will focus here on Cooper's proposal.⁵ The ETE of a particular population, or, more importantly, of a particular genotypic or phenotypic subpopulation, at a particular time and in a particularly specified environment, is just the probability-weighted sum of possible time intervals that might elapse before the (sub)population in question goes extinct. That is,

$$ETE_{x,e} = \sum_{t=0}^{\infty} p_t t,$$

where x is a particular (sub)population, e a particular environment, and p_t the probability of extinction in the t -th time interval (e.g., the t -th generation or t -th season). Although Cooper does not mention it, ETE_x , in order to represent anything like the fitness of x , must assume no source of new members of x except via reproduction of previous members. For example, recurrent mutation and migration alone must not be sustaining x 's duration. ETE_x is intended to represent the physical propensity of x -type organisms to endure via reproduction.

The first lesson to be drawn from this brief discussion of ETE is that there are probabilistic alternatives to 'the' propensity interpretation of fitness; ETE is one of many. The relative significances and roles of these various interpretations in evolutionary explanations beg for further clarification. Are these various alterna-

long-term evolutionary success, one can also distinguish between short-term and long-term fitness: between probable descendant contribution in the short term and probable descendant contribution in the long term (e.g., Mills and Beatty 1979). The relevant sort of fitness to invoke in order to explain short-term evolutionary success is short-term fitness; long-term fitness is most relevant to long-term success. In the apparent counterexamples just discussed, the inappropriate sort of fitness was invoked. In those cases, decreased long-term fitness should have been invoked to explain decreased long-term evolutionary success.

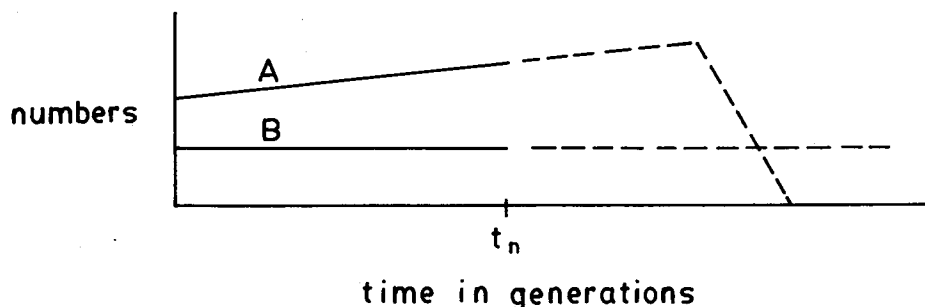
This rather casual acknowledgement of the need to distinguish probable descendant contribution in the short and long terms underscores the depth of the multiple propensities problem, showing the potential infinity of definitions hidden in the term 'descendant contribution'. We can create as many distinct such definitions as there are potential future generations and stages of the life cycle (see also Kitcher 1987, pp. 86–87). And shortly we will show how the family of probable descendant contribution interpretations must be extended even further – indeed, much further!⁸

But the difficulty that the short-term/long-term distinction presents for 'the' propensity interpretation is actually more complicated. In order to avoid the apparent problem of explaining low long-term evolutionary success in terms of high short-term fitness, we are supposed to invoke long-term fitness instead. But the fact is that, in some cases, such as those just considered, high short-term fitness indeed *explains* low long-term success. It may, for instance, just be the inability of parents to care sufficiently for large numbers of offspring that explains why organisms that leave too many offspring do not have many descendants in the long term. And inasmuch as high short-term fitness causally underlies low long-term fitness (and hence low long-term success) in such cases, reference to high short-term fitness constitutes a deeper explanation of the phenomenon than reference to long-term fitness. In short, the apparent counterexamples in which fitness is negatively correlated with evolutionary success are not so easily circumvented.

One response to this dilemma is to deny that short-term fitness is a legitimate notion, reserving the term 'fitness' for a long term propensity such as ETE. Thoday and Cooper argue for this approach, claiming that long-term ability to obtain representation has a more legitimate claim to the nomenclature 'fitness' than short-term ability. Since this approach would resolve the multiple propensity problem, it deserves consideration.

The sorts of cases we have been considering, in which high short-term fitness is compatible (indeed causes) low long-term success might be considered by proponents of long-term notions of fitness to be arguments *ad absurdum* against short-term notions of fitness. Let us consider such an example more closely. Suppose there are two genotypes, A and B, where A organisms are presently capable of leaving more offspring than B organisms, and are in fact doing so, even though we have grounds for inferring that A's fate will change. Suppose that we

can extrapolate as follows from the successes of A and B to date:



At time $t_n = \text{now}$, a defender of the distinction between long-term and short-term fitness might say that A has higher short-term fitness than B, but lower long-term fitness. But others will insist that B is *simply* fitter than A. A's greater initial frequency and relatively higher offspring contribution ability *mask* its lower fitness, i.e., its lesser ability to persist. Far from granting that A has high short-term and low long-term fitness, and especially far from granting that A's short-term fitness plays a deeper role in explaining its evolutionary success or failure, such evolutionary biologists and philosophers will deny that the term 'fitness' even applies to short-term ability to gain representation. According to this line of reasoning, the only viable notion of fitness as probable descendant contribution is one where probable descendant contribution refers to a sufficiently large number of generations hence.

While it seems plausible to suggest that 'fitness' should refer to the long-term in the sort of case just considered, this approach leaves us without an adequate account of a wide variety of evolutionary changes that require appeal to fitness. Most prominent among these are many short-term, micro-evolutionary explanations that clearly require reference to fitness. We sometimes want to know what it is about some phenotype or genotype that accounts for its *sudden* increase or decrease in frequency. ETE has nothing to say about such fluctuations.

The problems of ETE as the privileged interpretation of fitness run even deeper. Consider that we can use short-term fitness (whether high or low) to explain long-term fitness and long-term success, but we cannot use long-term fitness to account for short-term fitness or short-term success. So, short-term fitness actually seems to be explanatorily more powerful.

The problem with ETE as 'the' interpretation of fitness is somewhat the same problem as that of the long-run frequency interpretation of probability as expressed by Keynes, namely, that 'in the long run, we're all dead'. There is much about what happens in the meantime that is important and interesting to explain. ETE fails as a guide to understanding all aspects of fitness for much the same reason that frequency interpretation of probability fails as a guide to life.

But if ETE fails as the definition of 'fitness', so does expected offspring

contribution. What is needed is a more comprehensive analysis that takes into account both short- and long-term evolutionary success. As we shall argue, the problem of accommodating both short- and long-term evolutionary success in the definition of 'fitness' is one dimension of a much broader problem.

Supervenience and fitness components

The causal bases of fitness-qua-probable-descendant-contribution are multiple and multilayered. Possession of a particular pigment may underlie the camouflage that underlies the increased viability that contributes to the increased descendant-contribution ability of organisms of the appropriately pigmented type. A faulty meiotic mechanism may underlie the decreased fertility that detracts from the descendant-contribution ability of organisms of that type. Levels of viability, fertility, etc. are said to be causal 'components' of fitness; by the same token, camouflage (in this particular case) is a causal component of viability, and particular properties of the meiotic mechanism are causal components of fertility. Similarly, for those who respect the distinction, short-term fitness may be considered a causal component of long-term fitness.

Hand-in-hand with 'the' propensity interpretation of fitness goes the understanding that fitness cannot be universally expressed as any particular function of its components and subcomponents. Of course, the manner in which any organism achieves high fitness is a matter of its viability, fertility, etc., and ultimately a matter of the physical and chemical properties that underlie its viability, fertility, etc. levels. And yet different organisms achieve high fitness (and low fitness) in very different physical-chemical ways. What one member of a species accomplishes by increased viability, another may accomplish by increased fertility. What one accomplishes in terms of viability by way of possessing a particular pigment, another may accomplish by way of increased metabolic efficiency. And so on. So while each and every manifestation of high fitness can be explained in terms of underlying components and subcomponents of fitness, there seems to be no particular function of components and subcomponents in terms of which fitness can universally be expressed. Rosenberg (1985) speaks of the 'supervenience' of fitness upon its underlying causal components in his discussions of this aspect of fitness.

A criticism of 'the' propensity interpretation that we have already considered can now be restated and strengthened. Those who identify fitness with long-term ability to achieve representation might complain that supporters of the propensity interpretation, especially those who elaborate it in terms of probable *offspring* contribution, are mistakenly trying to construe fitness as a simple function of one of its *components*, namely short-term ability to achieve representation. In the process, supporters of the propensity interpretation overlook the fact that fitness is super-

sive analysis that takes into
 ess. As we shall argue, the
 evolutionary success in the
 der problem.

contribution are multiple and
 underlie the camouflage that
 the increased descendant-
 ly pigmented type. A faulty
 tility that detracts from the
 it type. Levels of viability,
 fitness; by the same token,
 component of viability, and
 usual components of fertility.
 ort-term fitness may be con-

f fitness goes the understand-
 any particular function of its
 nner in which any organism
 rtility, etc., and ultimately a
 nderlie its viability, fertility,
 h fitness (and low fitness) in
 member of a species ac-
 mplish by increased fertility.
 ay of possessing a particular
 ed metabolic efficiency. And
 h fitness can be explained in
 of fitness, there seems to be
 ents in terms of which fitness
 aks of the 'supervenience' of
 discussions of this aspect of

ve have already considered can
 fitness with long-term ability
 orters of the propensity inter-
 of probable *offspring* contribu-
 simple function of one of its
 epresentation. In the process,
 the fact that fitness is super-

venient upon, and hence not expressible as a simple function of, its components.

What is, to us, a much stronger criticism of 'the' propensity interpretation – perhaps the very most compelling criticism of that interpretation as it is usually elaborated – takes the same form, namely, of pointing out that the propensity interpretation mistakes a component of fitness for fitness itself. To see what component is at issue here, it is first necessary to recall some important details of the propensity interpretation. We can think of descendant contribution as an event with different outcomes o_1, o_2, \dots, o_n . Each outcome o_i represents a total contribution of i descendants. Now, given a particular organism x , there is a certain probability, p_1 , that o_1 will obtain. And there are probabilities p_2, p_3, \dots, p_n that outcomes

o_2, o_3, \dots, o_n will obtain. These probabilities represent x 's various propensities, based ultimately on physical-chemical properties of x , to leave various numbers of descendants. So, for example, the descendant contribution propensities of an imaginary organism x might be expressed in terms of the following probability distribution:

number of offspring	1	2	3	4	5	6	7	8	9
probability (x)	0.05	0.05	0.05	0.2	0.3	0.2	0.05	0.05	0.05

This distribution can be referred to as the offspring probability distribution of x . Alternatively, x can be a type – genotype or phenotype – of organism, in which case the various p_i represent average descendant-contribution probabilities.

One might think that such a distribution provides an adequate, albeit awkward, characterization of offspring contribution propensities. But beyond its unwieldiness, there is a problem in determining how to compare such distributions. For instance, is x fitter than, less fit, or equal in fitness to y and z , whose offspring probability distributions are as follows?

number of offspring	1	2	3	4	5	6	7	8	9	10
probability (y)					1.0					
probability (z)			0.5		0.3					0.2

In order to facilitate fitness comparisons, supporters of the propensity interpretation standardly move away from identifying fitness with entire probability distributions to identifying it with one particular statistic on the distribution, namely, the arithmetic mean, or 'expected value' (e.g., Brandon 1978, Mills and Beatty 1979). On such a construal, x , y , and z all have the same fitness (5.0), even though they have very different distributions. But of course there are many statistics on a probability distribution: the expected value, the mode, the median, the variance, the skew, etc. Why reduce fitness distributions to just one of these statistics? There are, after all, interesting differences between the descendant-contribution abilities of x ,

y, and z. Organism or type y will always leave 5 descendants, while z has a large chance of leaving a slightly smaller number, but also a small chance of leaving a much larger number. Is it legitimate to overlook these differences if our aim is to understand differences in the actual evolutionary successes of x, y, and z? As Rosenberg and Williams (1986) so pointedly put the question, is evolutionary expectedness no more and no less than mathematical expectedness?

No, in fact. Much work has recently gone into demonstrating that expected offspring contribution alone is sometimes poorly correlated with actual evolutionary success, even very short-term evolutionary success. For example, Gillespie (1974) has argued that organisms or types with the same expected offspring contributions can have very different actual evolutionary successes, depending on the variances of their offspring probability distributions. He argues in particular that of two organisms or types with the same expected offspring contribution, the one with smaller variance in its distribution will be evolutionarily more successful. An organism or type with a smaller expected value can even be more successful evolutionarily as long as its variance is also sufficiently smaller.⁹

A simulation example illustrates that variance in addition to expected value may be important in accounting for evolutionary success. This example (and all the others that follow) oversimplify natural processes in certain ways that do not allow us to generalize on the basis of them. But their purpose is just to serve as counterexamples to certain proposed definitions of fitness, not to serve as grounds for any new definition.¹⁰ Let us consider a population composed only of two asexual, haploid genotypes A and B, each initially represented by 10 organisms (i.e., initially at equal, 50%, frequencies). Suppose now that they have the same expected offspring contribution, but that their offspring probability distributions differ in the following manner:

number of offspring	1	2	3
probability (A)		1.0	
probability (B)	0.5		0.5

The expected offspring contributions of A and B are both 2.0, but the variances in their fitness distributions differ greatly: the variance of A being 0.0, while the variance of B is 1.0. Now consider what their evolutionary successes would be if the variation in B's offspring contribution were distributed between generations only. That is, while every A in every generation leaves 2 offspring, all the B's of one generation leave either 1 or 3 offspring – in approximately half the generations, B's leave 1 offspring per capita, and in the other half they leave 3 (the order in which the variation of B's offspring contribution is distributed is irrelevant – let us suppose alternating generations of 3 and 1 offspring per capita). The evolutionary success of A and B can be charted as follows for 10 generations:

Generation	A	B
0	10	10
1	20	30
2	40	30
3	80	90
4	160	90
5	320	270
6	640	270
7	1,280	810
8	2,560	810
9	5,120	2,430
10	10,240	2,430

By the end of 10 generations, the frequency of B has decreased from 50% to 19%.

What Gillespie, and this example, show is, in effect, that expected offspring contribution is just one component of fitness, variance is another. Fitness is supervenient upon each of its components, and hence cannot be expressed as a simple function of any one of them in particular (like expected value), or any particular combination of them.

One can even construct examples where two asexual haploid genotypes with the same expected offspring contributions and the same variances in their fitness distributions nonetheless have very different evolutionary successes, as long as the skew (assymetry) of the fitness distribution of one exceeds that of the other. For instance, consider the types C and D whose fitness distributions are as follows:

number of offspring	0.83	1.0	2.0	2.17	3.0
probability (C)		.6	0.3		.1
probability (D)	.5			.5	

The expected values of both are 1.5. The variance of C is 0.45 and that of D is 0.449. C's distribution, however, is skewed, with its right tail extending farther beyond its mean than does its left tail. D's distribution is not skewed. Now if we begin again with 10 C's and 10 D's, and if we suppose again that the variation in each of their offspring contributions is distributed wholly between generations, then we can chart their evolutionary successes as follows:

C's leave 1 offspring for the first 6 generations, 2 offspring for the next 3 generations, and 3 offspring the last generation.

D's leave 0.83 offspring for the first 5 generations and 2.17 offspring for the next 5 generations.

Generation	C	D
0	10	10
1	10	8.3
2	10	6.8
3	10	5.7
4	10	4.7
5	10	3.9
6	10	8.5
7	20	18.5
8	40	40.2
9	80	87.3
10	240	189.5

C, whose distribution has the greater skew, also has the greater evolutionary success.

One can even show that of two types with the same expected offspring contributions, the type with considerably smaller variance will have considerably less evolutionary success than the type with larger variance, as long as the latter has sufficiently greater skew. Consider, for instance, E and F, whose fitness distributions are as follows:

number of offspring	2.5	3.0	5.0	7.5	10.0
probability (E)		.5	.3		.2
probability (F)	.5			.5	

Here the expected values of E and F are both 5.0. The variance of E is 7.0 and that of F, 6.25. Suppose we begin again with 10 E's and 10 F's, and suppose again that the variation in the offspring contribution abilities is distributed wholly between generations:

E's leave 3 offspring for the first 5 generations, 5 offspring for the next 3 generations, and 10 offspring for the next 2 generations.
F's leave 2.5 offspring for the first 5 generations, and 7.5 offspring for the next 5 generations.

Generation	E	F
0	10	10
1	30	25
2	90	63
3	270	156
4	810	391
5	2,430	977

6	12,150	7,324
7	60,750	54,931
8	303,750	411,987
9	3,037,500	3,089,904
10	30,375,000	23,174,316

Fortunately, there is one statistic, geometric mean, that can be used in place of the combined three we have considered thus far (arithmetic mean, or expected value, variance, and skew) to predict evolutionary success in some of the sorts of scenarios we have been discussing. As Crow and Kimura (1970) among others argue, when offspring contribution varies between generations, geometric mean is the most appropriate predictor of evolutionary success. Indeed, under those circumstances, the geometric mean of A (2.0) is higher than for B (1.7), C (1.4) is higher than D (1.3), and E (4.4) is higher than F (4.5).

The problem that the use of geometric means introduces is just that they alone are appropriate only when a type's offspring contribution varies solely *between* generations. When a type's offspring contribution varies solely *within* generations (as in the second case involving A and B above), expected value, or arithmetic mean, is the better predictor of evolutionary success. But offspring probability distributions alone give us no indication of how a type's variation in actual offspring contribution will be distributed. The distribution alone does not tell us whether actual variation will be distributed mainly within or mainly between generations, or which of an infinite variety of combinations thereof will obtain. From the offspring probability distribution of genotype B, for instance, we cannot tell which of the following cases will obtain:

Case 1. Approximately half the B's of each generation leave 1 offspring, and half leave 3.

Case 2. In approximately half of all generations, B's leave 3 offspring, in the other half B's leave 1.

Case 3. In approximately half of all generations, half of the B's leave 1 offspring and half leave 3; in approximately one-quarter of the remaining generations, B's leave 3 offspring, and in the other quarter of generations, B's leave 1 offspring.

Case 4. In each generation, approximately one-quarter of the B's leave 1 offspring and one-quarter leave 3; the other half leave 3 offspring in half the generations, and 1 offspring in the other half.

The evolutionary successes of A and B differ from case to case in each of these four scenarios, as is easy to demonstrate. Thus, we cannot represent fitness (even short-term fitness) merely in terms of probability distributions of offspring contributions; we must also specify whether the variation in those distributions is

F
10
25
63
156
391
977

is the greater evolutionary

expected offspring contribu-
will have considerably less
ce, as long as the latter has
d F, whose fitness distribu-

0.0
.2

variance of E is 7.0 and that
D F's, and suppose again that
distributed wholly between

5 offspring for the next 3
ons.
d 7.5 offspring for the next 5

distributed within or between generations. If we know how the variation is in fact distributed (within or between generations), then we might be able to argue for the appropriateness of the geometric mean or the arithmetic mean as representing fitness. But it is often very difficult to determine this (as if it were not difficult to determine the distribution itself!), and there is even the possibility that a type switches reproductive strategies over time. In short, we may sometimes have no access to the sort of information we need in order to decide what statistic on the fitness distribution to employ in order to explain a particular evolutionary phenomenon.

There are other, perhaps more difficult, problems arising from the need to choose between different statistical representations of fitness (we do not aim to be comprehensive here). Consider, for instance, that within one population, there may be one type whose offspring-contribution variation is distributed wholly within generations, and whose fitness is (let us say) best represented by the arithmetical mean of that distribution; while in the same population there is another type whose offspring-contribution variation is distributed wholly between generations, and whose fitness is accordingly better represented by the geometrical mean of that distribution. These two types may have the same fitness, and may in the long run of generations enjoy the same relative evolutionary success. But in the short term, from generation to generation, their evolutionary successes may differ drastically in ways that reflect the differences between the types. More specifically, the type whose offspring-contribution variation is distributed between generations will periodically lag behind the success of the other type for a few or even many generations, depending on the range of the former type's offspring-contribution variation. Now if we really care to understand very short-term (down to one generation?) differences in evolutionary success in terms of fitness differences, then the multiple propensities problem (in this case as represented by the geometric mean vs. the arithmetic mean calculation of fitness) is going to cause difficulties.

A different perspective on basically the same problem is to imagine the alternative sorts of stochastic effects that infringe upon the evolutionary successes of the two types under discussion. If the two types are present in very large numbers, then there should be only negligible stochastic effects on the evolutionary success of the type whose offspring-contribution variation is distributed wholly within generations. But over a short number of generations, there may still be great stochastic effects on the evolutionary success of the type whose offspring-contribution variation is distributed between generations. Again, because of the multiple propensities problem, we must sometimes infer different evolutionary successes on the basis of identical fitness values.

The problems involved in choosing one or another statistic to calculate fitness aside, though, it is crucial to recognize that such choices will arise. The various statistics on fitness distributions, such as the geometric or arithmetic mean, the variance and the skew, are aspects of an organism's or type's reproductive strategy,

and as such are components of fitness – they contribute to evolutionary success in different ways, depending upon the environmental (broadly construed) circumstances. Once it is acknowledged that these statistics represent components of fitness, it becomes apparent that identifying fitness generally with any one statistic, or any particular function of statistics, is mistaken. We stand to learn a great deal about fitness and its role in evolution by studying descendant-contribution distributions, how they bear upon evolutionary success, and how they may be compared.

Conclusion

To decide a priori that fitness is a propensity to contribute descendants to the next generation, or to the tenth generation, or to the thousandth generation, is to beg important questions that are rightfully settled in terms of the sorts of evolutionary questions we pose for ourselves. To decide a priori that fitness is to be identified with one particular statistic (or one particular function of statistics) from a probability distribution of descendant contributions is to beg further important questions that are rightfully settled empirically, in ways that depend upon the organisms and environments we are investigating. The propensity interpretation of fitness, as usually articulated, is shortsighted in both of these respects.

Nothing in the above analysis suggests that fitness is not a propensity. But 'fitness' does seem to stand for a very broad family of propensities – a family that is difficult to describe in general terms. It would be unfair to suggest that, lacking any generally agreed-upon definition of 'fitness', we therefore lack *any* understanding of evolution in terms of fitness differences and natural selection. On the other hand, until we have an appropriate general definition of fitness, it is not altogether clear *how much* we understand about evolution in terms of fitness differences and natural selection. Our aim here is not just to be pessimistic about prospects in this regard; rather, our aim is to be realistic. General satisfaction with the propensity interpretation of fitness has created, we believe, a false sense of understanding. There is clearly room for improvement.

Notes

1. We are grateful to Peter Abrams and Robert Brandon for helpful discussions concerning the issues treated here.
2. See Brandon 1978, Mills and Beatty 1979, Burian 1983, Sober 1984, Kitcher 1987, and Mayr 1988. This list is meant to be exemplary, not complete.
3. See Rosenberg 1985, Rosenberg and Williams 1986, and Hodge 1987. Again, the list is exemplary, not complete.
4. See the examples discussed in Mills and Beatty 1979.
5. See also the excellent discussion of alternative notions of fitness in Endler 1986.
6. This is just one sense of 'evolutionary success'; another would be speciation rate. But

we will confine our discussion to the micro-evolutionary sense.

7. The literature on evolution of clutch size contains many such discussions. See, for example, Lack's classic 1947, also Lack 1954, 1966, 1968. For a useful, brief summary, see Pianka 1978, pp. 135–138.
8. We are leaving out of our discussion ways in which the family of propensities that constitute fitness might need to be extended still further to cover different units of selection.
9. Several discussions with Robert Brandon over the past several years have been very helpful in developing the views that follow. Brandon also encouraged us to use simulation examples to illustrate the issues in question; in fact, the first of the following examples is his. He plans to discuss similar topics in his book, in preparation, *Adaptation and Environment*.
10. We will not refer to any actual taxa here – of course, that is nothing to brag about. For literature dealing with real organisms, see the excellent review by Seger and Brockmann 1987.

References

- Brandon R. (1978). Adaptation and evolutionary theory. *Studies in History and Philosophy of Science* 9: 181–206.
- Burian R. (1983). Adaptation. In Grene M. (ed.) *Dimensions of Darwinism: Themes and counterthemes in twentieth century evolutionary theories*. Cambridge: Cambridge University Press.
- Cooper W.S. (1984). Expected time to extinction and the concept of fundamental fitness. *Journal of Theoretical Biology* 107: 603–629.
- Crow J., Kimura M. (1970). *An introduction to population genetic theory*. Minneapolis: Burgess.
- Endler J.A. (1986). *Natural selection in the wild*. Princeton: Princeton University Press.
- Darwin C. (1859). *On the origin of species*. Facsimile edition by Harvard University Press, Cambridge, 1959.
- Gillespie J.H. (1973). Natural selection for within-generation variance in offspring number. *Genetics* 76: 601–606.
- Hodge M.J.S. (1987). Natural selection as a causal, empirical, and probabilistic theory. In Krüger, L. et al. (eds.) *The probabilistic revolution*, Volume 2. Cambridge: MIT Press.
- Kitcher P. (1987). Why not the best? In J. Dupré (ed.) *The latest on the best: essays on evolution and optimality*. Cambridge: MIT Press.
- Lack D. (1947). The significance of clutch size. *Ibis* 89: 302–352.
- Lack D. (1954). *The natural regulation of animal numbers*. Oxford: Oxford University Press.
- Lack D. (1966). *Population studies of birds*. Oxford: Oxford University Press.
- Lack D. (1968). *Ecological adaptations for breeding in birds*. London: Methuen.
- Mills, S., Beatty J. (1979). The propensity interpretation of fitness. *Philosophy of Science* 46: 263–286.
- Pianka E.R. (1978). *Evolutionary ecology*. New York: Harper and Row.
- Rosenberg, A. (1985). *The structure of biological science*. Cambridge: Cambridge University Press.
- Rosenberg A., Williams M.B. (1986). Discussion: fitness as primitive and propensity. *Philosophy of Science* 53: 412–418.
- Seger, J., Brockmann J. (1987). What is bet-hedging? *Oxford Surveys in Evolutionary Biology* 4: 182–211.
- Sober E. (1984). *The nature of selection: a philosophical inquiry*. Cambridge: MIT Press.
- Thoday J.M. (1953). Components of fitness. *Symposia of the Society for Experimental Biology* 7: 96–113.