OPTIMAL-DESIGN MODELS AND THE STRATEGY OF MODEL BUILDING IN EVOLUTIONARY BIOLOGY*

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The prevalence of optimality models in the literature of evolutionary biology is testimony to their popularity and importance. Evolutionary biologist R. C. Lewontin, whose criticisms of optimality models are considered here, reflects that "optimality arguments have become extremely popular in the last fifteen years, and at present represent the dominant mode of thought."

Although optimality models have received little attention in the philosophical literature, these models are very interesting from a philosophical point of view. As will be argued, optimality models are central to evolutionary thought, yet they are not readily accomodated by the *traditional* view of scientific theories. According to the traditional view, we would expect optimality models to employ general, empirical laws of nature, but they do not. Fortunately, the *semantic* view of scientific theories, a recent alternative to the traditional view, more readily accomodates optimality models. As we would expect on the semantic view, optimality models can be construed as specifications of ideal systems. These specifications may be used to describe empirical systems—that is, the specifications may have empirical instances. But the specifications are not empirical claims, much less general, empirical laws.

Although philosophers have yet to discuss the general features and uses of optimality models, these topics have stimulated much recent discussion among evolutionary biologists. Their discussions raise a number of precautions concerning the proper use of optimality models. Moreover, many of their caveats can be interpreted as general reminders that 1) optimality models specify ideal systems whose empirical instantiations may be quite restricted, and that 2) optimality models should not be construed as general, empirical laws. As G. F. Oster and E. O. Wilson caution, "the prudent course is to regard optimality models as provisional guides to further empirical research and not necessarily as the key to deeper laws of nature." It seems, then, that the semantic view of theories is more sensitive to the nature and limitations of optimality models than is the more traditional view of theories.

1. Introduction.

We are accustomed to thinking of evolutionary theory as a theory of change: change in the genotypic and phenotypic composition of

populations. Yet a great deal of what can surely be called "evolutionary theorizing" is devoted to the construction and analysis of non-dynamic models like Figure 1. These so-called "optimality models" provide evolutionary insight into the morphological and behavioral design of organisms, by describing fitness as a function of design variables, and by allowing the investigator to determine what combination of design-variable values maximizes fitness. The fitness-maximizing combination of variable values constitutes the so-called "optimal design". Where optimal designs are found in nature, their presence is presumed to be due to natural selection.

For example, with the help of the optimality model in Figure 1, Holling (1964) provided evolutionary insight into the predatory behavior of praying mantids. The figure shows a mantid foreleg grasping the largest prey which it can lock into place (that is, prey of this size, but no larger, have the minimum amount of contact with the femur, tibia, and tibial hook necessary to keep them locked in place). Through a geometrical analysis of the prey item in place, Holling was able to characterize the diameter of the prey as a function of various parameters of the foreleg anatomy: the diameter is simply $T \sin (\beta - \alpha)$, where T is the length AC, α is the angle BAC, and β is the angle
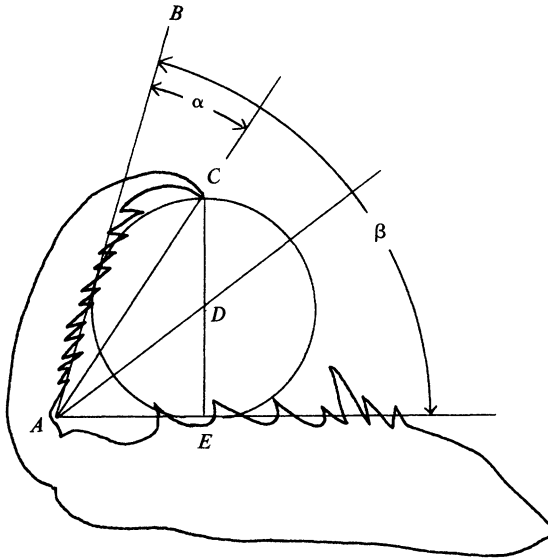

Figure 1:   Holling's (1964) geometric analysis of the optimal size of a prey item, given the anatomy of a praying mantid's foreleg. The optimal diameter is $T \sin (\beta - \alpha)$, where T is the length AC.

BAE (whose value can be calculated from the value of α). Holling reasoned that the capture of larger prey is more energy efficient (in terms of energy expended and energy consumed), and that fitness increases with energy efficiency. Thus, he argued, the optimal predatory behavior for mantids is to attack prey of diameter $T \sin (\beta - \alpha)$. And he found that, in fact, mantids most often attack prey of that size. Holling's model certainly provides a picturesque introduction to optimality models. A more detailed analysis of these models will be presented later.[1]

The prevalence of optimality models in the literature is testimony to their popularity and importance. Leading journals of evolutionary biology such as *American Naturalist, Annual Review of Ecology and Systematics,* and *Evolution* abound in articles on optimal predatory behaviors, optimal mate-selection behaviors, and optimal clutch size, to name just a few applications of optimality models. Evolutionary biologist, R. C. Lewontin, whose criticisms of optimality models will be considered in this paper, reflects that "optimality arguments have become extremely popular in the last fifteen years, and at present represent the dominant mode of thought". (1978a, p. 7)

Unfortunately, optimality models have received little attention in the philosophical literature.[2] Yet these models are very interesting from a philosophical point of view. As will be argued, these models are not readily accommodated by the traditional view of scientific theories, according to which we would expect the models to employ general, empirical laws of nature. Instead, optimality models are best construed as specifications of ideal systems which may be used to

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[1]The optimality approach to the understanding of nature may bring to mind the natural theological tradition, according to which optimal design was taken as evidence of the work of an intelligent Creator. Paley's *Natural Theology* (1802) is a classic example of this sort of reasoning. All, if anything, that remains of this approach in modern optimality analyses is the heuristic "God's eye" perspective. As Oster and Wilson describe the approach of the optimality analyst, he

> "plays God": he designs the biological system, including as many of the relevant quantities as possible and then checks to see if his own optimal design is close to that observed in nature. If the two correspond, then nature can be regarded as reasonably well understood. (1978, p. 299)

In the modern context, though, optimal design is a sign of evolution by natural selection rather than God's intelligent design. As Oster and Wilson are quick to add, optimality analyses are methods of "making educated guesses as to how evolution might have proceeded."

[2]This assessment must be qualified. Interpretations of sound design are certainly at issue in the often discussed role of teleological reasoning in modern biology (see especially Hull 1974, Mayr 1961, Munson 1971, Ruse 1973, Williams 1976, Wimsatt 1972, and Wright 1976). But in these discussions, it is generally just assumed that appropriate design models can be constructed, and the structure of the models is not discussed in any detail.

represent empirical systems, but which do not specify their own empirical range of applicability. In this regard, at least, optimal-design theorizing represents an instance of the sort described by the semantic view of theories, a recent alternative to the traditional view. The semantic view itself, and reasons for preferring the semantic view of optimality models, will be discussed in detail.

Although philosophers have yet to discuss the general features and uses of optimality models, these topics have stimulated much discussion among evolutionary biologists, ecologists, and anthropologists.[3] Some of their analyses are extremely critical, and some are mildly precautionary. But all emphasize limits to the proper use of optimality models. Many of their caveats can be interpreted as general reminders that optimality models specify ideal systems and should not be construed as general, empirical laws of nature.

2. The Adaptive-Landscape and Semantic Views of Optimality Models.

2.1 We need to describe the structure of optimality models more precisely than we have so far. In particular, we need to differentiate the two main components of every optimality model: 1) the design problem to be solved, and 2) the set of feasible solutions under consideration. Ideally, the design problem expresses fitness as a function of particular design variables. However, variables which vary proportionately with fitness may be substituted for fitness. For example, the design problem of Holling's model expresses energy efficiency as a function of prey-size choice. Inasmuch as fitness is supposed to increase with energy efficiency, Holling's design problem at least indirectly expresses fitness as a function of prey-size choice.

In analyzing or solving a design problem, one attempts to determine which combination of design-variable values results in the greatest fitness value. If fitness has been replaced by another variable which varies proportionately with fitness, then one attempts to determine which combination of design-variable values leads to the greatest or smallest value of the substituted variable, depending on whether that variable varies directly or inversely with fitness.

The solutions to these maximization or minimization problems are "constrained," however, in the sense that the design variables related to fitness cannot assume just any values. Instead, the values of each variable are constrained to a range of physically feasible values, the specification of which constitutes the second component of a biological

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[3]See especially Gould and Lewontin (forthcoming), Lewontin (1977, 1978a, 1978b), Maynard Smith (1978), Oster and Wilson (1978), Stearns (1977), and Sahlins (1976).

optimality model. For instance, one very common constraint clause in optimality models is known as "the principle of the allocation of energy" (Cody 1966, p. 175; Gadgil and Bossert 1970, pp. 3–4). According to this almost self-evident principle, the values of many design variables, like clutch size and speed, are constrained by limited energy resources which must be allocated to all design variables. Solutions to optimal-design problems are also constrained by mechanical factors, wherein the values of certain design variables mechanically restrict the values which other variables can assume. For instance, the hard exoskeleton of insects restricts their overall growth and limits the total number of eggs that can be carried at one time (Stearns 1977, pp. 151–153). Mechanical constraints on design values also operate in Holling's model. For the nature of the grasping mechanism sets upper limits to the size of prey which can be captured.

  2.2 So far, we have characterized optimality models only in terms of their components: the design problem, and the set of feasible solutions under consideration. But we will now consider a graphical representation of these models as "adaptive landscapes." This sort of analysis is useful and interesting on several related counts. First, the adaptive-landscape approach provides a *uniform* means of representing all optimality models (including Holling's, which, judging from its peculiar pictorial representation, would seem to have little in common with any other optimal-design models). Second, the adaptive-landscape approach is a *common* means of presenting optimality models (in fact, one of the models which we will be discussing in depth is often presented in the adaptive-landscape format). And third, intrinsically different kinds of explanation in evolutionary biology, of which optimal design analyses are one kind, can be distinguished in terms of their use of adaptive landscapes. Each of these points will emerge during this discussion.

  An adaptive landscape is an n-dimensional space, $n-1$ dimensions of which represent design variables, and the other dimension of which represents fitness. The space is contoured to represent fitness peaks and fitness valleys corresponding to various combinations of design-variable values. In the landscape of Figure 2, the horizontal and vertical axes represent two design variables x and y, so that each point in the x, y plane represents a design. The axis perpendicular to the x, y plane represents fitness, so that the heights of the contours represent the degrees of fitness of individuals possessing the corresponding x and y values.

  Adaptive landscapes were introduced by Wright (1932) as tools for the articulation and analysis of evolutionary problems. In fact, Wright first used such a diagram to help convey the evolutionary
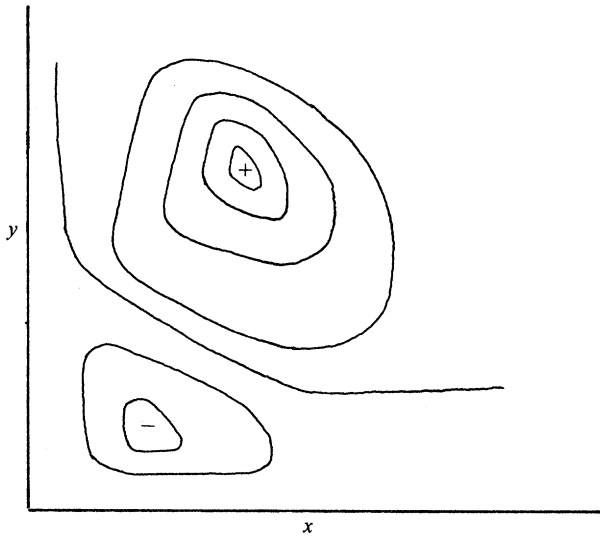
Figure 2:   Adaptive landscape. The horizontal and vertical axes represent design variables x and y. The axis perpendicular to the x,y plane represents fitness. The heights of the contours represent the degrees of fitness of individuals possessing the corresponding x and y values.

significance of natural selection as he conceived it then.

> In a rugged field of this character, selection will easily carry the species to the nearest peak, but there may be innumerable other peaks which are higher but which are separated by "valleys." (Wright 1932, pp. 358–359)

In other words, if the contours of an adaptive landscape correctly describe the relation between fitness and the design variables of the members of a species, then the peaks of the adaptive landscape indicate alternative outcomes of the evolution of that species, while the valleys represent temporary states through which the evolution of the species might pass.

We will return to the evolutionary insight gained from adaptive landscapes. But for now, it should be clear that whatever evolutionary insight is to be gained from adaptive landscapes can be gained from optimality models, since adaptive landscapes are just graphic representations of optimality models. The design problem of an optimality model, which expresses fitness as a function of design variables, is represented by the contours of the adaptive landscape. Although optimality models also place feasibility constraints upon the value

of each design variable, these constraints are not represented by many adaptive landscapes like Figure 2, but they can be added as boundaries around the feasible designs as in Figure 3.

Figure 3 is a complete optimality model in the adaptive-landscape format. In order to analyze this model—that is, in order to solve the design problem set by the model—we need only "look" to find the feasible x, y combination which corresponds with the greatest fitness value. That design is x_i, y_{fc}.[4]

Holling's model can also be reconstructed to fit the adaptive-landscape format (though more for the sake of uniformity than for any interesting results). This landscape will consist of only two dimensions, since the design problem expresses energy efficiency as a function of only one design variable: prey-size choice. Unfortunately, Holling

[4]The "adaptive-landscape" representation of optimality models is, in perhaps more familiar terms, a special "state-space" representation of those models. The n-1 design variables and fitness constitute an n-dimensional "space," the "states" of which are all the possible n-tuples, or combinations of design-variable values. The state-space representations of some theories specify successions of states which satisfy particular equations; while the state-space representations of other theories, including optimality models, specify the subsets of states which satisfy particular equations (see Section 3.1). Oster and Wilson (1978) describe optimality models in state-space terms.
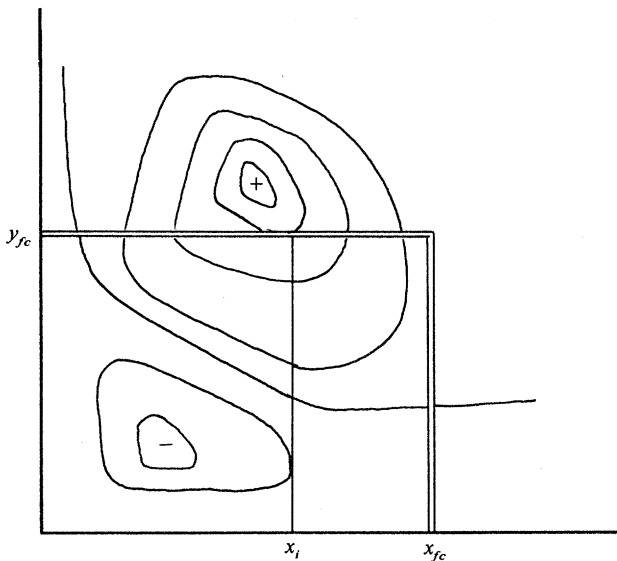

Figure 3:   Adaptive landscape with upper constraints x_{fc} and y_{fc} on values of x and y.

does not describe the exact relationship between energy efficiency and prey-size choice, so we do not really know how steep the peaks of the adaptive landscape are, though we do know that the elevation increases with the choice of larger prey. The feasibility constraints of Holling's model rule out prey diameters beyond $T \sin (\beta - \alpha)$, since beyond this value, the prey-grasping device is ineffective. Thus, a side-view, adaptive-landscape version of Holling's model looks something like Figure 4. The analysis of the model is simple enough: the optimal, feasible solution to the problem of prey-diameter choice is the choice of prey of diameter $T \sin (\beta - \alpha)$.

The adaptive-landscape approach has played a more significant role in the construction of other optimal-design theories, like optimal sex-ratio theory (MacArthur 1965, pp. 389–391; Leigh 1971, pp. 39–48). In an attempt to shed light on the predominance of 50:50 sex ratios in nature, evolutionary biologists have constructed three-dimensional adaptive landscapes, which express fitness as a function of two design variables: the number of male offspring x and the number of female offspring y.

Of course, not all male and female offspring combinations are physically feasible. There are certainly constraints on the total number of offspring k which an organism can produce and rear. So we can assume that there are upper limit constraints of the form $x + y = k$ upon the male and female offspring combinations of any parent.

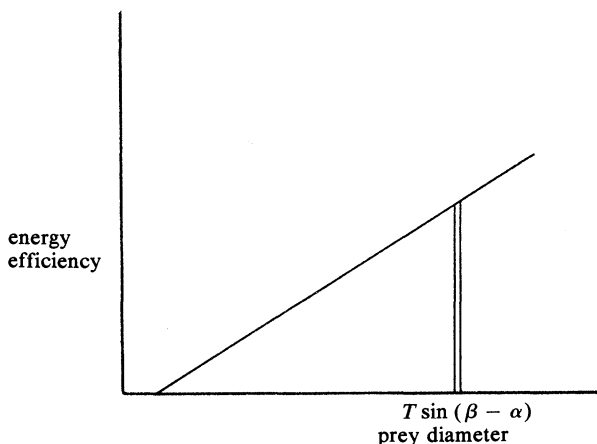$$T \sin (\beta - \alpha)$$
prey diameter

Figure 4: A side-view, adaptive-landscape representation of Holling's optimality model. The design problem is represented by the sloping energy-efficiency, prey-diameter relationship. The design constraints are represented by the upper boundary ($T \sin (\beta - \alpha)$) on prey-diameter values.

The design problem of the optimal sex-ratio model is provided by the claim that parental fitness increases as the product of the number of male offspring times female offspring (xy) increases (MacArthur 1965, pp. 389–391; Leigh 1971, pp. 39–48). The argument leading to this conclusion is complicated, and since the details are not necessary for our present purposes, the argument has been placed in Appendix 1.

What concerns us now is finding a solution to the design problem from among the set of feasible solutions. To solve this problem, we must first sculpture the three-dimensional space defined by the two design variables and fitness into an adaptive landscape which reflects the relation between fitness and those design variables, as that relation is described by the design problem. Given that parental fitness is purported to increase as the product of the number of male offspring times female offspring increases, the contours of our adaptive landscape will represent different values of the product xy. The resulting landscape is pictured in Figure 5.

It is easy to see that the feasible x, y combination with the greatest fitness value is the point at which the contour $xy = c$ is tangent to the feasibility constraint $x + y = k$. This point is midway along $x + y = k$, where $x = k/2$ and $y = k/2$. Thus, the optimal male-female combination is one-half male and one-half female. And this corresponds to the 50:50 sex ratios which are so prevalent among species of sexual organisms.

2.3 The general trend in contemporary philosophy of biology has been to characterize biological theories, not just in terms of their intrinsically peculiar characteristics, but also as "scientific" theories, by demonstrating that biological theories satisfy all the conditions of a legitimate scientific theory.[5] In keeping with that trend, we will now characterize optimal-design theories from a general view of scientific theories. But the view of scientific theories to be employed is not the view traditionally employed. Differences between the alternative view—the so-called "semantic view" of theories—and more traditional views will be discussed presently. But reasons for preferring a semantic rather than a traditional view of optimality models will be postponed until after we have discussed the current critiques of optimality models. The advantage of the semantic view, in this case at least, is that it is more sensitive to the critiques of optimality models.

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[5]The finest examples of this trend include Hull (1974), Munson (1975), Ruse (1973), and M. B. Williams (1970, 1973, 1974, 1977, forthcoming).

By way of very brief introduction, the semantic view seems to be so called in order to distinguish it from the so-called "received view" of scientific theories, which characterizes theories both syntactically and semantically. Since this distinction provided the stimulus for the development of the semantic view, a thorough characterization of the semantic view would focus on the differences between the semantic and received views. But here again the details are not necessary for our present purposes, and so have been placed in Appendix 2. For our purposes, the differences between the semantic view and another traditional view—one often conjoined with the received view—are more important, even though this distinction may not have been crucial in the development of the semantic view.

According to tradition, theories currently used for purposes of explanation must be syntactically structured and semantically interpreted in such a way that among their axioms and theorems are what are thought to be general, empirical laws of nature (e.g., Hempel 1965; Popper 1934). To say that the axioms and theorems are general is just to say that they are either universal generalizations (of the form "all instances of kind A are instances of kind B") or statistical generalizations (of the form "$X\%$ of the instances of kind A are instances of kind B"). To say that the axioms and theorems are empirical is to say that their truth or falsity does not depend on the meanings of their constituent terms and/or their logical form alone (that is, they are not analytically true or contradictory); experientially discernable features of the world are also relevant to their truth or falsity. To say that the axioms and theorems are supposed to be laws of nature is to say that they are supposed to be true, not only in the weak sense that there have never been exceptions to the generalizations, but also in the stronger sense that exceptions to the generalizations are considered physically impossible. As Hempel suggests, a statement "will not count as a law if it rules out certain hypothetical occurrences which an accepted theory qualifies as possible." (1966, p. 58)[6]

The alternative, semantic view of theories was originally outlined by P. Suppes (1957, 1967a, 1967b), and has since been developed in various directions by Sneed (1971), Stegmüller (1976), F. Suppe (1972), and van Fraassen (1970, 1972). Giere's discussion of theories in his introductory text for the philosophy of science (1979) is perhaps

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[6]M. B. Williams's (1970, 1974) axiomatization of Darwinian evolutionary theory is an elegant example of the analysis of a biological theory in terms of the "received" and "traditional" views of theories. Ruse (1973) also combines both views in an analysis of population genetics.
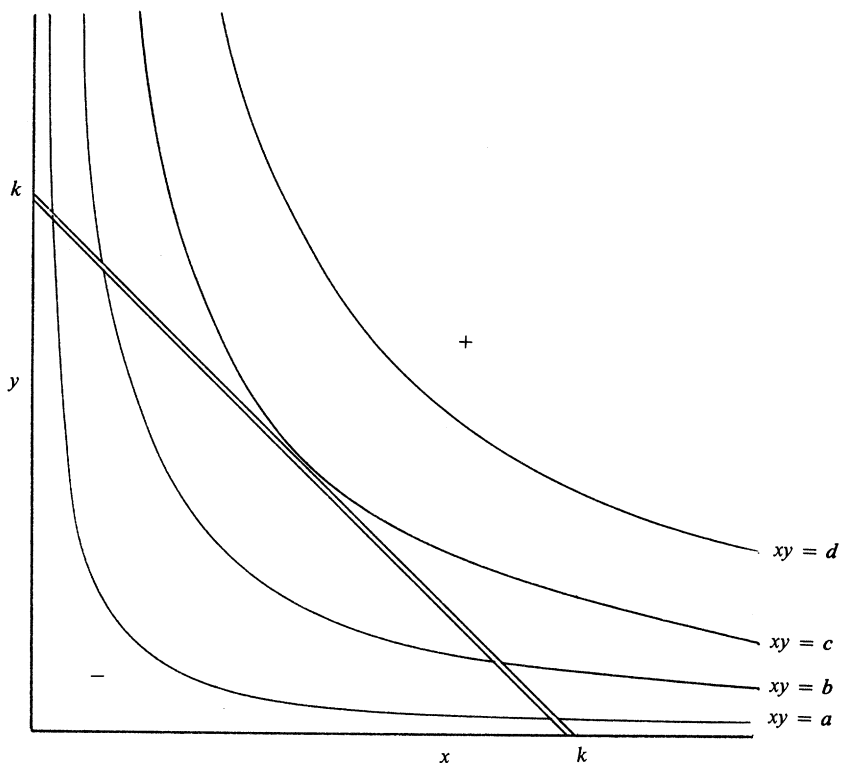
Figure 5: Optimal sex-ratio model in the adaptive-landscape format. The design problem is represented by the contours $xy = a$, $xy = b$, $xy = c$, etc., each of which represents x,y combinations of equal fitness. Contour $xy = c$ represents x,y combinations of greater fitness than those of $xy = b$, and of still greater fitness than those of $xy = a$.

the simplest version of the semantic view. There are differences, to be sure, between the views which these authors have proposed, but there is a central significant thesis. As van Fraassen suggests,

> Like Suppes, I shall take it that (the "pure" part of) a theory defines the kind of system to which it applies; empirical assertions would take the form that a given empirical system belongs to such a kind . . . . (1972, p. 311)

This view is clearly an alternative to the traditional view of theories, because, according to this view, theories do not consist of empirical claims, much less general, empirical laws of nature. Rather, theories stipulatively specify kinds of systems. This is an empiricist philosophy of science, however. It is just that the empirical claims of science

are not considered to be components of theories. Rather, the empirical claims of science are made on behalf of theories. They assert that particular empirical systems are instances of the kinds of systems stipulatively specified by theories. These empirical claims provide the explanatory link between the theories and the behavior of empirical systems. For having identified an empirical system as an instance of a specified kind, an investigator can then account for aspects of the behavior of the empirical system in terms of the consequences of its being an instance of the specified kind.[7]

For example, we can regard our optimal sex-ratio theory as just the specification of a kind of system: namely, the kind described by Figure 5. We need not regard it as a set of general, empirical laws. After all, what is Figure 5 other than just the specification of a kind of system? The diagram itself does not specify that any particular kinds of empirical systems are subject to the constraint $x + y = k$ or to the rule that fitness increases as the product xy increases. Figure 5 merely specifies a kind of system in terms of these constraints and rules.

The empirical claims made on behalf of our optimal sex-ratio theory can possess any degree of generality. For example, we might make the restricted empirical claim that "Members of the species *Rattus rattus* satisfy the feasibility constraints and design problem of Figure 5." Or we might make the more general claim that "Members of all species satisfy the conditions of Figure 5." Although the optimal sex-ratio theory can be applied in some such manner, the theory itself does not specify its empirical range of applicability. In this sense, optimal-design theories specify "ideal" systems: kinds of systems which may or may not have empirical instances.[8]

As will be argued, current critiques of the use of optimality models can be construed as warnings that optimality models do not consist

[7]Of course, it is not likely that the specification of a system would ever be introduced *without* an empirical application of the specification. We certainly want to avoid the proliferation of *in*applicable system specifications. So although we may, on the semantic view, abstract system specifications from their applications, we should not expect to find specifications without applications in practice. Sneed's (1971) and Stegmüller's (1976) versions of the semantic view take into full account this close association of system specifications and empirical applications. On their "Kuhnian" version, theories are characterized not only in terms of the systems they specify, but also in terms of exemplary or paradigmatic applications of the system specifications. The paradigmatic applications may suggest further possible applications not originally associated with a system specification. Sneed's and Stegmüller's versions represent an important step in the direction of applying the semantic view to the dynamics (and not simply the structure) of science. For our present purposes, however, what is important about the semantic view is that it allows us to talk about science in terms of 1) system specifications and 2) empirical applications which may possess any degree of generality.

of general, empirical laws, and are more reasonably construed as specifications of ideal systems whose empirical instantiations may be quite restricted. We will turn to those critiques as soon as we have discussed the role of optimality models in evolutionary thought. For characterizing optimality models in terms of the semantic view of theories is just one way of responding to critiques of those models. Dispensing with the use of the models is another response, the plausibility of which requires an analysis of the role of optimality models.

3. The Role of Optimality Models in Evolutionary Thought.

3.1 The contribution of optimality models to evolutionary understanding may as yet be obscure, since these models concern static design considerations rather than change. Lewontin (1969) acknowledges this problem by distinguishing between two modes of theorizing in evolutionary biology, each of which employs a different adaptive-landscape approach. One mode of theorizing concentrates on the trajectory of a system across an adaptive landscape, specifying the historical sequence of states occupied by that system. This mode employs population-genetic theory to account for the trajectories through the phenotypic design space in terms of the origin and dynamics of genotypic variation. But although *ideal* systems can be specified in this manner, it is difficult to make reliable empirical claims on the basis of these specifications. For it is difficult to determine what kind of genotypic variation actually underlies the phenotypic variation in nature.

In the absence of this kind of information, we are forced to rely on a second mode of theorizing, which concentrates only on the structure of the adaptive landscape. This is the optimality model. Lewontin refers to it as a "short-cut" mode of evolutionary theorizing (1978a).

Optimality models provide "short-cut" accounts of evolution in

[8]Optimality models are certainly not the only theories which lend themselves to the semantic view. There seems to be no theory, and no area of research, which cannot be described in terms of the semantic view. Even an incomplete survey reveals the following wide range of applications: group theory (Suppes 1957, 1967b), Newtonian particle mechanics (Giere 1979, Sneed 1971, Stegmüller 1976, Suppes 1957, 1967b, and Wessels 1976), quantum mechanics (van Fraassen 1970, 1972), equilibrium thermo-dynamics (Moulines 1975), Mendelian genetics (Giere 1979), and population growth (Giere 1979). See also footnote 14.

the sense that they are often used to account for the *outcome* of evolution by natural selection, without reference to the *historical process* of evolution by natural selection. That is, a design shared by members of a population is often attributed to the effects of natural selection when 1) the design in question is optimal according to a particular optimality model, and 2) there is some support for an empirical claim on behalf of that optimality model, to the effect that members of the population in question approximately satisfy the constraints and conditions of the model. For example, on the basis of Holling's optimality model, prey-diameter choice among mantids of the species *Mantis crassa* can be attributed to natural selection, since their prey choice is optimal according to Holling's model, and since members of that species approximately satisfy the design constraints and design problem of the model. Similarly, on the basis of our optimal sex-ratio theory, the 50:50 sex ratio of many species can be attributed to natural selection, since a 50:50 sex ratio is optimal according to that model, and since the members of many species approximately satisfy the design constraints and design problem of that model.

Of course, an implicit premise in any such attempt to account for optimal design in terms of natural selection is an optimization principle to the effect that natural selection results in the predominance of the optimal forms. Actually, such a principle can be derived from the theory of population genetics. That is, it can be demonstrated that natural selection changes the genotype frequencies (and the corresponding phenotype frequencies) in such a way as to increase the average fitness of the population (see Appendix 3). So there is reason to believe that when a population satisfies the conditions of an optimality model, and when members of that population share the design which is optimal according to the model, the design in question owes its presence to natural selection.

It is important to keep in mind, however, that in light of the implicit optimization principle derived from population genetics, accounts of the outcome of evolution based on optimality models do not completely "short-cut" the dynamics of population-genetic theory. While optimality models themselves involve no assumptions about population dynamics, evolutionary accounts based on optimality models do involve such assumptions. Consequently, evolutionary accounts based on optimality models also do not short-cut the need for making difficult assumptions about the relation of the phenotypic variation under investigation to its underlying genotypic variation.

3.2 Lewontin suggests three reasons for the recent surge in popularity of optimality models in evolutionary biology. One reason, that

"optimality arguments dispense with the tedious necessity of knowing anything concrete about the genetic basis of evolution," has been shown to be true only in the limited sense that optimality models *themselves* have no genetic parameters, though evolutionary accounts based on optimality models certainly do involve genetic assumptions. Lewontin's second reason for the popularity of optimality models is that maximization principles have had general appeal in *many* sciences—not just in evolutionary biology (he cites Fermat's principle of least action, Hamilton's principle, and the idea of the "invisible hand" in economics). And Lewontin's third reason for the popularity of optimality models is that optimality arguments are fair game for everyone, since a healthy imagination is all that is required (Lewontin 1978a, p. 7). Leigh adds a fourth reason for the popularity of optimality models in the adaptive-landscape format. That is, simply, "biologists like pictures" (1979, p. 42).

But in addition to the "short-cut" accounts of evolution which optimality models provide, and in addition to the other suggestions as to their frequent use, optimality models play another very important role in evolutionary thought. The significance of optimal-design analyses for estimations of relative fitness is all too often overlooked. And since relative fitness is an important parameter of population-genetic theory, optimality models should not be looked upon simply as static *alternatives* to the dynamic, population-genetic mode of thought.

Perhaps the reason that the role of optimality models in comparisons of fitness is so often overlooked is that "fitness" is so often defined in terms of *success* at survival and descendant contribution, rather than in terms of *design* for survival and descendant contribution. As is common, the population geneticists Crow and Kimura regard fitness simply as "a measure of both survival and reproduction . . . " (1970, p. 5). Thus, survival rates and descendant tallies seem more appropriate than optimality models for comparisons of fitness.[9]

But a simple thought experiment suggests that this interpretation of fitness is incorrect, and that an interpretation of fitness in terms of design is necessary. Imagine that identical twins are standing together in a forest. As it happens, one of them is struck by lightning and killed, while the other survives. The latter matures, mates, and leaves descendants, while the former leaves no descendants. In this case, there are no physical differences between the twins which account for their differences in survival and descendant contribution. Yet

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[9]See also Dobzhansky (1970, pp. 101–102), Mettler and Gregg (1969, p. 93), Waddington (1968, p. 19), and Wilson (1975, p. 585).

given the usual definition of "fitness," the surviving twin is by far the fitter.[10]

If this result is counterintuitive, it must be for the reason that the abilities of the twins to survive and contribute descendants based on their physical designs were not taken into account. One may be prone to judge the twins equally fit, on the grounds that their similar designs rendered them equally capable of surviving and contributing descendants. As evolutionary biologist G. C. Williams states in response to the usual definition of "fitness,"

> . . . it focuses attention upon the rather trivial problem of the degree to which an organism actually achieves reproductive survival. The central biological problem is not survival as such, but design for survival. (1966, p. 159)

And as evolutionary biologist S. J. Gould also responds,

> . . . traits confer fitness by an engineer's criterion of good design, not by the empirical fact of their survival and spread. (1976, p. 26)

In accordance with this line of reasoning, it has been suggested that "fitness" does not refer to *actual descendant contribution*. Rather, "fitness" refers to *expected descendant contribution based on physical design* (Brandon 1978; Mills and Beatty 1979).[11] Thus, just as it is not sufficient to argue that the surviving twin is fitter on the grounds that it survived and left more descendants, it is also not sufficient to argue that organisms which choose prey of a certain size are fitter just because they leave more descendants. The twins are equally fit because their expected descendant contributions on the basis of

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[10]Brandon (1978, pp. 293–294), Hull (1974, p. 68), and Scriven (1959, p. 478) suggest similar thought experiments.

[11]As Mills and Beatty (1979) define "fitness,"

> The fitness of an organism x in environment E is $n = [df] n$ is the expected number of descendants which x will leave in E.

The expected number of descendants is calculated as follows. We can think of descendant contribution as an event with different outcomes O_1, O_2, . . ., 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_i that O_i will occur. And there are probabilities p_1, p_2, . . . , p_n that outcomes O_1, O_2, . . . , O_n will occur. The expected number of descendants of x, then, is the weighted sum,

$$p_1 O_1 + p_2 O_2 + \ldots + p_n O_n.$$

Each of the probabilities p_1, p_2, . . . , p_n is based on the physical design of x, just as the probability that a die will land with a certain side up is based on the physical design of the die.

their identical physical designs are equal. Similarly, organisms with the predatory behavior in question are fittest because expected descendant contribution is a function of prey-size choice, and (given that function) the prey-size choice in question maximizes expected descendant contribution. Thus, optimal-design models are particularly suitable for comparisons of fitness.

Of course, differences in the actual survival and descendant contributions of differently designed organisms may be used as evidence in favor of differences in their fitness, especially when quantitatively precise differences are needed, and/or when we do not know how the design differences might be related to fitness differences. But the use of such data requires at least the *assumption* that the differences in actual success are due to differences in design.

4. Current Critiques of Optimality Models

4.1 Having argued that optimality models are central to evolutionary thought, it is now necessary to take into account current critiques of those models. The criticisms which will be considered here are directed specifically at the design problems of optimality models. These criticisms will be interpreted as general reminders that optimal-design problems cannot reasonably be construed as general, empirical laws of nature. In light of these criticisms, it will be urged that the semantic view of theories provides a more reasonable strategy for the construction and use of optimality models than does the traditional view of theories.[12]

Before discussing the criticisms of optimal-design problems, it will be helpful to consider the reasons why the feasibility constraints of optimality models cannot reasonably be construed as general, empirical laws. This brief discussion will help to show why design problems also cannot be construed as laws.

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[12]In addition to criticisms of the design problems, several other criticisms have been levelled at optimality models. For example, it is often objected that some evolutionary explanations in terms of optimality models involve unjustified assumptions about the genetic bases of the designs in question (Lewontin 1978a; Maynard Smith 1978; Oster and Wilson 1978). It is also often objected that some proponents of evolutionary explanations in terms of optimality models continually avoid refutations of their accounts through *ad hoc* amendments of their accounts (Gould and Lewontin, 1979; Lewontin 1977, 1978a, 1978b). Finally, it is often objected that optimality models are used too often in accounts of evolution because of the common but incorrect view that all designs in nature owe their presence to natural selection (Gould and Lewontin forthcoming; Lewontin 1977, 1978b). However, these criticisms are better directed at the methodological scruples and theoretical presuppositions of the *proponents* of these illegitimate uses of optimality models than at optimality models themselves. And since these criticisms have been treated in depth in the sources listed, they will not be treated here.

As was discussed earlier, when trying to determine what combination of design-variable values results in the greatest fitness of an organism, we must keep in mind that there are restrictions upon the values which the design variables in question can assume. These constraints arise from an interaction of the traits in question with other traits. This interaction may be "energetic," in the sense that there is a limited amount of energy available for the development and expression of the sum traits of an organism. This interaction may also be "mechanical," in the sense that the development and expression of the traits in question is mechanically constrained by the development and expression of other traits.

At any rate, since the form of the constraint is presumably due to the particular interaction of traits, the form of the constraint can vary as the interaction varies, and hence as the traits interacting vary. And since we have reason to believe that a population may vary and evolve with respect to any of the traits of its members, we also have reason to believe that the form of the constraints on any set of design variables can also vary. Thus, we must not regard the design constraints of our optimality models as laws of nature. For although they may be true of certain populations at certain times, we have reasons to believe that exceptions to the constraints are evolutionarily (not just logically) possible.

For example, it may presently be true that praying mantids cannot capture prey of diameter greater than $T \sin (\beta - \alpha)$, since their prey-grasping devices presently fail at greater diameters. But given selective adjustments of their prey-grasping devices—e.g., given greater curvature of the femur to match that of the tibia—mantids might be able to catch prey of diameter greater than $T \sin (\beta - \alpha)$. Since these selective adjustments are evolutionarily possible, we must consider it possible that exceptions to the present constraints might arise. So we cannot consider the present constraint a law of nature.

Similarly, the constraint in our optimal sex-ratio model should not be considered a law of nature. That constraint, $x + y = k$, is supposed to signify that the only restriction upon the number of male and female offspring which a parent can leave is a restriction upon the *total* number. But it may be the case, in some species, that it is more difficult to bear and rear females, so that the restriction on the total number of female offspring differs from the restriction on the total number of male offspring. Differential mortality among males and females between the times of fertilization and conception might account for such a difference (Mayr 1939 discusses this possibility). For such a population, the proper constraint would be of the form $x + Ay = k$, where $A > 1$.

Not only is it evolutionarily possible for design constraints to differ from population to population, but the constraint on any one population may change over time (which is presumably why constraints would differ from population to population). So, again, we should not regard the feasibility constraints of optimality models as laws of nature. And, as is about to be seen, there are similar reasons for not construing the design problems of optimality models as laws.

4.2 Common to several critiques of optimality models is a distrust of the design problems specified by the models. In each case, as we shall see, the critics point out that the form of the design problem can vary with variations in originally unspecified design variables. Granting this point for the moment, and granting that a population can vary and evolve with respect to any of the design variables of its members, it follows that the form of any design problem can vary. So for basically the same reasons that we must avoid construing feasibility constraints as laws of nature, we must also avoid construing design problems as laws. For although design problems may be true of certain populations at certain times, we have reason to believe that exceptions to the problems are evolutionarily possible.

Consider, first, Sahlins's argument, that it is a fallacy to express fitness as a function of any one subset of design variables, and thus a fallacy to associate maximum fitness with any particular combination of design-variable values (1976, pp. 82–83). For as Sahlins suggests, the number of additional, alternative paths to maximum fitness increases with the number of additional design variables considered.[13]

Sahlins's argument is in response to an optimality analysis proposed by G. C. Williams, on the basis of which the atrophy of the digestive tract of salmons is explained as the product of natural selection (Williams 1966, p. 174). According to Williams, the atrophy of the system just before spawning time is optimal given that salmons reproduce only once, because the degeneration provides materials and space for the formation of gametes, and unburdens the salmons of extra weight which hinders their trips upstream toward the spawning grounds. Sahlins's rejoinder is worth quoting in full:

> As a representation of natural selection, the fallacy of this reasoning, which might be called "the fallacy of an *a priori* fitness course," is fairly evident. The several difficulties are summed up by the question, if selection will go so far as to atrophy the digestive tract in favor of a single reproductive explosion that

[13]Sahlins is an anthropologist, rather than an evolutionary biologist, whose criticisms of optimality models were inspired by the frequent use of those models in sociobiology.

kills the organism, why should it not as easily effect structural changes that will allow the salmon to spawn twice or more to the same fitness effect, as for instance sturgeons do? The problem is that this course or some other was precluded not by a natural selection but by an artificial one. The salmon was taken as an *a priori* limited being with only one possible solution to the evolutionary problem of resource allocation to fitness, by a premise not motivated in the nature of evolution itself. (Sahlins 1976, pp. 82–83)

In all fairness to Williams, Sahlins's argument is not quite to the point. Sahlins chides Williams for not considering the optimality of multiple spawnings as an evolutionary *alternative* to single spawnings. Of course, Williams is aware of this alternative but is, for the moment, only concerned with the optimality of traits *correlated* with spawning just once. But Sahlins's argument raises an interesting point. And that is, that the relationship between an organism's fitness and a subset of its design variables will be stable only as long as other, perhaps unspecified design variables of the organism are held constant. Certainly Williams's proposed relationship between fitness and digestive-system atrophy is conditional upon spawning once and no more. But what other design constants does the proposed relation rely on? Another way of asking this question is, what selective adjustments, other than an increase in spawning times, might increase fitness and at the same time preserve the digestive system? An increase in parental investment devoted to the development of the young might, for instance, increase fitness and yet require the preservation of the digestive system. A clever biologist might invent any number of alternatives to the atrophy of the digestive system by selectively varying unspecified design variables. After all, how many alternative means are there to any end? If, as seems reasonable, it is assumed that the form of a design problem always depends upon unspecified design variables, then exceptions to any design problem will be evolutionarily quite possible. For, as Sahlins put it, the invariance of the unspecified variables is "a premise not motivated in the nature of evolution itself."

Oster and Wilson (1978) emphasize the same limitation on optimal-design problems, pointing out that for any given design problem, and hence for any optimal design, evolution can always provide alternative optimal solutions. As Oster and Wilson stress,

The very combinatoric richness of the possible permutations in the genetic code makes it impossible to enumerate even a small fraction of the allowable strategies [i.e., alternative solutions to a design problem]. The essentially innovative nature of the

evolutionary process precludes an exhaustive list of allowable
strategies. The strategy set is always changing, new ones being
added and old ones deleted. On the face of it, this property appears
to be incompatible with the requirements of optimality models,
since the strategy set cannot be specified *a priori*. (Oster & Wilson
1978, p. 299)

Lewontin sums up the difficulties in formulating reliable design
problems by noting that their reliability depends upon whether the
relation of the chosen design parameters to fitness is independent
of the values of any unspecified design variables (1977; 1978b, p.
230). But we have no more reason to believe that evolution will ensure
the permanence of any such temporary independence, than we have
reason to believe that evolution will ensure the invariance of unspecified
design variables. So although we may formulate *temporarily* reliable
design problems, we cannot formulate reliable design *laws*.

One way of protecting our design problems from the sort of
evolutionarily possible exceptions we have been discussing is by
appending an appropriate *ceteris paribus* clause to each problem. The
design problems would then take the form of a conditional to the
effect that fitness can be expressed as a particular function of specified
design variables, as long as no unspecified design variables disturb
the relation between fitness and the specified variables. Lewontin
suggests this way out.

> In order to make an argument that a trait is an optimal solution
> to a particular problem, it must be possible to view the trait
> in isolation, all other things being equal. If all other things are
> not equal, if a change in a trait as a solution to one problem
> changes the organism's relation to other problems of the environ-
> ment, it becomes impossible to carry out the analysis part by
> part, and we are left in the hopeless position of seeing the whole
> organism as being adapted to the whole environment. (Lewontin
> 1978b, p. 220)

Lewontin is unenthusiastic about the use of the *ceteris paribus*
condition, however, since he feels that it renders applications of design
problems unfalsifiable (1977). That is, the applicability of an optimal
design problem to members of a particular species can be defended
even when members of the species share a nonoptimal trait, since
it can always be argued that some unspecified traits disturbed the
proposed relationship between fitness and the specified design vari-
ables. So any alternative design problem can just as well be applied

to members of the species, since none of the alternatives can be falsified.

Philosophers of science have expressed similar reservations about the use of *ceteris paribus* clauses. For example, Hempel argues that,

> . . . no empirical evidence can ever disconfirm a hypothesis of this form since an apparently unfavorable finding can always be attributed to a violation of the *ceteris paribus* clause by the interference of factors other than those specifically included in [the antecedent conditions]. (Hempel 1952, p. 167)

The usual rejoinder to this scepticism is that hypotheses with *ceteris paribus* qualifications can be falsified as long as the *ceteris paribus* conditions can be spelled out in terms of a finite list of possible interfering factors (e.g., Coffa 1973). When a hypothesis is qualified in this manner, we need only check for the presence of each of the listed possible interfering factors to determine whether apparently unfavorable findings should be attributed to a violation of the *ceteris paribus* clause or to a violation of the hypothesis.

Unfortunately, optimal-design models cannot be qualified by such specific *ceteris paribus* clauses. For we cannot specify all the possible combinations of additional design-variable values that might interfere with the proposed relation between fitness and the originally specified design variables. In the first place, as Oster and Wilson urged, the "essentially innovative process of evolution" precludes a finite list of evolutionarily possible designs. The list of possible interfering design-variable values will be as long as our imaginations are healthy.

But in the second place, it is not even clear that organisms have a countable number of design variables (Pratt 1972). So the list of possible interfering design-variable values might be uncountably long. For whatever reason, we cannot protect optimal design problems from evolutionarily possible exceptions by qualifying them with a finite number of *ceteris paribus* conditions.

The dangers of regarding optimal-design problems as reliable laws of nature are amply demonstrated by recent arguments to the effect that the design problem of our optimal sex-ratio model is not generalizable. It was originally thought that sex ratios among all species could be explained on the grounds that fitness increases as the product of the number of male and female offspring increases; differences in sex ratio were assumed to be due to different feasibility constraints. But Trivers and Willard (1973) recently proposed an alternative design problem which they believe is not only evolutionarily possible, but is the correct relation of fitness to male and female offspring ratios among certain species of mammals. According to Trivers and Willard's

alternative design problem, fitness among normally healthy females may increase as the number of their male offspring increases. And fitness among unhealthy females may increase as the number of their female offspring increases. Thus, by considering the effect on fitness of an originally unspecified design variable (namely, the health of female parents), an alternative design problem is recognized not only as an evolutionary possibility, but also as an evolutionary actuality. (The reasoning behind this alternative design problem is outlined in Appendix 4.)

4.3 If there is a lesson to be learned from current critiques of optimality models, surely the lesson is that we cannot characterize those models in the same manner that scientific theories have traditionally been characterized. That is, we have little reason to believe that optimality models are syntactically structured and semantically interpreted in such a way that their axioms and theorems are general, empirical laws of nature. However, an alternative to a traditional view of optimality models is available in the semantic view of theories. On the semantic view, a theory is not comprised of general, empirical laws. Rather, a theory is just the specification of an ideal system which may be used to represent empirical systems, but which does not specify its own empirical range of applicability. Given that optimality models in their usual adaptive-landscape format simply specify a kind of system, it seems reasonable that we should characterize those models in terms of the semantic view of theories. Given that optimality models cannot be construed as general, empirical laws, there is further reason to characterize them in terms of the semantic view.

The semantic view also satisfactorily accomodates the explanatory use of optimality models. On the semantic view, having identified an empirical system as an instance of a specified kind, an investigator can then account for aspects of the behavior or nature of the empirical system in terms of the consequences of its being an instance of the specified kind. The empirical instantiation need not be lawlike in order to play an explanatory role. Similarly, having ascertained that a population satisfies the constraints and conditions of an appropriate optimality model, an investigator can then account for the presence of optimal design among members of the population in terms of the population's being an instance of the kind specified by the model. The sort of insight gained from ascertaining that the population satisfies the conditions of the optimality model does not depend on the existence of a law of nature to that effect. In fact, we may presume that the relation between fitness and the design variables in question will change in time, as evolutionary changes occur with regard to unspecified design variables.

Of course, even the harshest critics of optimality models acknowl-
edge that those models can *sometimes* be used to represent nature.
For instance, Lewontin admits that to disregard the presence of optimal
designs in nature would be "to throw the baby out with the bathwater."
To account for these designs, we must admit that the relations of
the design variables in question to fitness were "quasi-independent"
of unspecified design-variable values for a sufficient length of time
(Lewontin 1978b, p. 230). But we need not regard the appropriate
design problems as timeless laws.

In conclusion, we *need not* regard optimality models, or even claims
made on their behalf, as laws of nature. And given the evolutionary
contingency of feasibility constraints and design problems in nature,
we *should not* regard optimality models or claims made on their behalf,
as laws of nature. We should recognize them as specifications of
ideal systems. And we should be careful in applying them to nature,
making only such restricted empirical claims on their behalf as are
suggested by the evidence. This approach, which is at odds with
the traditional view of scientific theorizing, is nevertheless consistent
with the alternative, semantic view. This approach is also in keeping
with the opinion of Oster and Wilson, who summarize their critique
of optimality models by strategizing that,

> . . . the prudent course is to regard optimality models as provisional
> guides to future empirical research and not as the key to deeper
> laws of nature. (Oster and Wilson 1978, p. 312)[14]

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[14]Work in progress involves a more extensive analysis of evolutionary theory in
terms of the semantic view of theories, and a more extensive critique of the traditional
view of evolutionary theory (e.g., Beatty forthcoming). Traditional axiomatizations
of evolutionary theory have taken two forms: either the principle of natural selection
is the logical core of the theory (e.g., Williams 1970, 1974), or the principles of population
genetics are the logical core (e.g., Ruse 1973). But there are difficulties in construing
either axiom set as laws of nature. The purported tautological status of the principle
of natural selection is well known (but see Brandon 1978 and Williams 1974). Moreover,
Mendel's first law, from which the principles of population genetics are derived, describes
a genetically based trait subject to evolutionary changes, and thus is a description
of evolutionary happenstance rather than a physically necessary regularity.

The problem of evolutionary laws does not arise for semantic representations of
evolutionary theory, however. On the semantic view, evolutionary theory may be
construed as a non empirical specification of a natural-selection system and/or a
Mendelian breeding system. Empirical instantiations of the specifications provide the
explanatory link between the theories and the behavior of empirical systems. For
having identified an empirical system as an instance of a natural-selection system
and/or a Mendelian breeding system, an investigator can then account for the
evolutionary behavior of the empirical system in terms of the consequences of its
being an instance of the specified kind. This is, of course, just a sketch of an argument,
the details of which are forthcoming.

Appendix 1. Leigh's (1970) argument that fitness increases as the product of the number of male offspring times female offspring increases. First, suppose that there are upper limits to the total number of offspring k which an organism can leave, and that these constraints are of the form $x + Ay = k$, where x is the total number of male offspring and y is the total number of female offspring. In other words, A sons can be raised for every one daughter. Note that the product xy, or $y(k-Ay)$, is maximized when $y = k/2A$ and $x = k/2$. So *if* fitness is maximized when xy is maximized, then the optimal x and y values will be $y = k/2A$ and $x = k/2$, or in other words, A times as many sons as daughters. The question now is whether parents with these x and y values have a greater fitness (a greater expected number of descendants—see Section 3.2) than parents with any other feasible x, y values.

Let us imagine a population of individuals which are subject to the constraint $x + Ay = k$, but which do not contribute A times as many sons as daughters. Let us suppose that they contribute $A + z$ times as many sons as daughters. So where X is the total number of male offspring of one generation of this population, and Y is the total number of female offspring, $X = (A + z)Y$.

Now let us introduce into this population a family of the supposedly optimal proportions: $k/2$ sons and $k/2A$ daughters. And let us compare the expected genetic contribution q of this family to the expected genetic contribution q' of the average family of the population, whose composition will be $k(A + z) / (2A + z)$ sons and $k/(2A + z)$ daughters. (To compute the average family composition, solve $x + Ay = k$ for x and y, given that $x = (A + z)y$ and $y = x/(A + z)$.)

In order to compute the expected descendant contribution of the supposedly optimal family, consider that the generation g of the progeny of that family includes the $k/2$ sons of the family, $X = (A + z)Y$ males not sons of the family, the $k/2A$ daughters of the family, and Y females not daughters of the family. The members of generation $g + 1$ will owe half their heritage to the males and half to the females of generation g. Thus, the proportion of generation $g + 1$ that is descended from the supposedly optimal family will be the average of the proportions of the sons and daughters of the optimal family among all the males and females of generation g:

$$q = (1/2)\left[\frac{k/2}{k/2 + (A + z)Y}\right] + (1/2)\left[\frac{k/2A}{k/2A + Y}\right]$$

$$= (1/2)\left[\frac{1}{1 + 2Y(A + z)/k} + \frac{1}{1 + 2AY/k}\right].$$

Similarly, the proportion of generation $g + 1$ that is descended from any average family will be:

$$q' = (1/2)\left[\frac{k(A + z)/(2A + z)}{k(A + z)/(2A + z) + (A + z)Y}\right] + (1/2)\left[\frac{k/(2A + z)}{k/(2A + z) + Y}\right].$$

$$= (1/2)\left[\frac{1}{1 + Y(2A + z)/k} + \frac{1}{1 + Y(2A + z)/k}\right].$$

If we let $B = (2A + z)Y/k$, and $C = zY/k$, we obtain:

$$q = \frac{1 + B}{(1 + B)^2 - C^2}, \text{ and}$$

$$q' = \frac{1}{1 + B}.$$

Thus, q is greater than q'. So the family of supposedly optimal composition actually has a greater expected descendant contribution than a family of any other composition (Leigh 1971, pp. 45–46).

Appendix 2. The received view of theories and the semantic view of theories. The "semantic view" of theories is so called in order to distinguish it from the so-called "received view" of theories, which characterizes theories both syntactically and semantically. On the received view, the initial syntactic characterization of a theory consists in specifying what is known as an axiomatic calculus, which has four main components: 1) a vocabulary, or list of signs to be used in the formulation of the theory, 2) formation rules which govern the arrangement of signs into well-formed formulas, 3) a given set of well-formed formulas to be taken as axioms, and 4) rules of inference which license the inference of particularly structured, well-formed formulas from others (formulas derived from the axioms by the specified rules of inference are known as theorems).

This syntactic characterization is then followed by a semantic interpretation wherein the signs of the axiomatic calculus are interpreted as referring to various empirical entities and attributes. Only as a result of this interpretation do any of the axioms and theorems become empirical statements—statements whose truth or falsity is contingent upon empirical states of the world. Of course, proponents of the received view are most interested in interpreting the signs of the calculus in such a way that the axioms and theorems correctly describe the empirical entities and attributes designated by their terms. Such interpretations are said to delineate the "models" of a theory, where a model of a theory can be construed as a kind of system correctly described by the theory. (At this point, we must differentiate the latter philosophical use of the term "model" from the biologists' informal use of the term—as in "optimality model"—though we will see shortly that the two uses of the term are not so different after all.)

But this syntactic-semantic picture of theories raises an interesting problem. For standard formulations of most theories (in textbooks, etc.) do not assume the form of axiomatic calculi with appended interpretations. Indeed, it is questionable whether some theories (things we call "theories") like much of evolutionary theory, Freudian psychology, theories of the origin of the universe, and many others, can be characterized in this manner at all. At least, we are in a position to ask whether, and/or how we might construct axiomatic calculi for different theories. And this suggests that there must be some means of characterizing and differentiating theories other than *via* their interpreted calculi. As Suppes expressed the problem in an article entitled "What is a Scientific Theory?" (1967),

> The formulation of a theory as a logical calculus or, to put it in terms that I prefer, as a theory with standard formalization, gives an intrinsic characterization, but this is not the only approach. For instance, a natural question to ask is whether a theory *can* be axiomatized within standard formalization, that is, within first order logic. In order to formulate such a question in a precise manner, it is necessary to have some extrinsic way of characterizing the theory. (Suppes 1967, p. 60)

As an alternate means of characterizing a theory, Suppes proposed that we simply specify the intended models of a theory (i.e., a semantic characterization), without reference to any particular axiomatic calculus (i.e., without a syntactic characterization). In other words, we are to characterize theories simply as specifications of the kinds of systems to which they can be applied. As van Fraassen relates the task of theories according to this characterization,

> From this point of view, the essential job of a scientific theory is to provide us with a family of models, to be used for the representation of empirical phenomena. On the one hand, the theory defines its own subject matter—the kinds of systems that realize the theory; on the other hand, empirical assertions have a single form: the phenomena can be represented by the models provided. (van Fraassen 1972, p. 310)

Since, on this view, theories are simply specifications of models, and since the specification of models is a matter of semantics, the "semantic view" of theories

is an appropriate means of reference. (As is argued in Sections 2.3 and 4, optimality models simply specify the kinds of system to which they can be applied. Thus, optimality models, in the informal biological sense of "model", are actually model specifications, in the formal, philosophical sense of "model". So the semantic view of theories provides a nice explication of the notion of an optimality *model*.)

Appendix 3. Optimization principles in population genetics. In order to see how natural selection changes genotype frequencies in such a way as to increase the average fitness of a population, let us consider a one-gene locus which is occupied by only two genes B and b. The proportions of B and b are p and q respectively ($p + q = 1$). Now consider the following general selection model:

genotype	BB	Bb	bb
initial frequency	p^2	$2pq$	q^2
relative average fitness	W_1	W_2	W_3
proportionate contribution to next generation	$p^2 W_1$	$2pq W_2$	$q^2 W_3$
proportion in next generation	$\dfrac{p^2 W_1}{\bar{W}}$	$\dfrac{2pq W_2}{\bar{W}}$	$\dfrac{q^2 W_3}{\bar{W}}$

The quantity $\bar{W}$ is simply the sum of the proportionate contributions of BB, Bb, and bb. That is, $\bar{W} = p^2 W_1 + 2pq W_2 + q^2 W_3$. This quantity is often referred to as the "average fitness of a population" because it is a weighted sum of the fitness values W_1, W_2, and W_3 (weighted in terms of the proportions of BB, Bb, and bb).

Two straightforward consequences of this model are the following:

$$\triangle p = pq \left[\frac{p(W_1 - W_2) + q(W_2 - W_3)}{\bar{W}} \right], \text{ and}$$

$$\triangle q = pq \left[\frac{p(W_2 - W_1) + q(W_3 - W_2)}{\bar{W}} \right]$$

(where $\triangle p$ and $\triangle q$ represent changes in frequency of B and b in one generation—for a derivation, see Mettler and Gregg 1969, pp. 96–97). What is particularly interesting about these equations is that, when the numerator of the right side of the equation is held constant, $\triangle p$ and $\triangle q$ are inversely proportional to $\bar{W}$ or average fitness. Thus, according to the general selection model, the higher the mean fitness, the slower the evolutionary change, and the lower the mean fitness, the faster the evolutionary change. As Mettler and Gregg conclude,

> ... the rate of change in gene frequency slows down as the mean fitness increases toward its maximum, and the rate is faster when the population is far away from its "potential" reproductive capability. This is akin to the statement made previously that selection tends to maximize the fitness of the population, i.e., the gene frequency continues to change as long as $\bar{W}$ is not the largest value possible. (Mettler and Gregg 1969, p. 97)

Li (1955) demonstrated, on the basis of the principles of population genetics, that natural selection would not only increase the average fitness of a population, but

that under the influence of natural selection, the genotype frequencies of a population will achieve stable equilibrium when and only when the average fitness of the population is maximal ($\triangle q = 0$ if and only if $d\bar{W}/dq = 0$). However, as Li also pointed out, this optimization principle, as well as the optimization principle above, requires the assumption that the relative fitnesses of the genotypes is not a function of the frequencies of the genotypes. See Lewontin (1971) for further qualifications of the optimization principles of population genetics.

Appendix 4. Trivers and Willard's (1973) argument that when maternal health is poor, fitness increases as the number of female offspring increases; and when maternal health is good, fitness increases as the number of male offspring increases. Imagine a population of animals in which the health of adult females varies substantially. Let us suppose that a female in good health is better able to bear and rear her offspring than is a female in poor health. And let us also suppose that at the end of the period of parental care, the healthiest offspring will tend to be offspring of the adult females who were in the best condition during the period of parental care. Finally, let us suppose that such differences in condition among the offspring affect the male offsprings' reproductive success more than they affect the female offsprings' reproductive success. For example, males in good health may tend to exclude other males from breeding altogether. Given these assumptions, an adult female in good health who bears a son will leave more grandchildren than a similar female who bears a daughter. And an adult female in poor health who bears a daughter will leave more grandchildren than a similar female who bears a son (Trivers and Willard 1973, p. 90).

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