OPTIMIZATION THEORY   ♦4134
IN EVOLUTION

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INTRODUCTION

In recent years there has been a growing attempt to use mathematical methods borrowed from engineering and economics in interpreting the diversity of life. It is assumed that evolution has occurred by natural selection, and hence that complex structures and behaviors are to be interpreted in terms of the contribution they make to the survival and reproduction of their possessors—that is, to Darwinian fitness. There is nothing particularly new in this logic, which is also the basis of functional anatomy, and indeed of much physiology and molecular biology. It was followed by Darwin himself in his studies of climbing and insectivorous plants, of fertilization mechanisms and devices to ensure cross-pollination.

What is new is the use of mathematical techniques such as control theory, dynamic programming, and the theory of games to generate a priori hypotheses, and the application of the method to behaviors and life history strategies. This change in method has led to the criticism (e.g. 54, 55) that the basic hypothesis of adaptation is untestable and therefore unscientific, and that the whole program of functional explanation through optimization has become a test of ingenuity rather than an enquiry into truth. Related to this is the criticism that there is no theoretical justification for any maximization principles in biology, and therefore that optimization is no substitute for an adequate genetic model.

My aim in this review is not to summarize the most important conclusions reached by optimization methods, but to discuss the methodology of the program and the criticisms that have been made of it. In doing so, I have taken as my starting point two articles by Lewontin (54, 55). I disagree with some of the views he expresses, but I believe that the development of evolution theory could benefit if workers in optimization paid serious attention to his criticisms.

I first outline the basic structure of optimization arguments, illustrating this with three examples, namely the sex ratio, the locomotion of mammals, and foraging behavior. I then discuss the possibility that some variation may be selectively neutral, and some structures maladaptive. I summarize and comment on criticisms made by Lewontin. The most damaging undoubtedly is the difficulty of testing the

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hypotheses that are generated. The next section therefore discusses the methodology of testing; in this section I have relied heavily on the arguments of Curio (23). Finally I discuss mathematical methods. The intention here is not to give the details of the mathematics, but to identify the kinds of problems that have been attacked and the assumptions that have been made in doing so.

THE STRUCTURE OF OPTIMIZATION MODELS

In this section I illustrate the argument with three examples: (a) the sex ratio, based on Fisher's (28) treatment and later developments by Hamilton (34), Rosado & Robertson (85), Trivers & Willard (96), and Trivers & Hare (95); (b) the gaits of mammals—given a preliminary treatment by Maynard Smith & Savage (66), and further analyzed in several papers in Pedley (78); (c) foraging strategies. Theoretical work on the latter subject originated with the papers of Emlen (27) and MacArthur & Pianka (57). I have relied heavily on a recent review by Pyke et al (81). These authors suggest that models have in the main been concerned with four problems: choice by the animal of which types of food to eat (optimal diet); choice of which patch type to feed in; allocation of time to different patches; pattern and speed of movement. In what follows, I shall refer only to two of those—optimal diet and allocation of time to different patches.

All optimization models contain, implicitly or explicitly, an assumption about the "constraints" that are operating, an optimization criterion, and an assumption about heredity. I consider these in turn.

The Constraints: Phenotype Set and State Equations

The constraints are essentially of two kinds. In engineering applications, they concern the "strategy set," which specifies the range of control actions available, and the "state equations," which specify how the state of the system being controlled changes in time. In biological applications, the strategy set is replaced by an assumption about the set of possible phenotypes on which selection can operate.

It is clearly impossible to say what is the "best" phenotype unless one knows the range of possibilities. If there were no constraints on what is possible, the best phenotype would live for ever, would be impregnable to predators, would lay eggs at an infinite rate, and so on. It is therefore necessary to specify the set of possible phenotypes, or in some other way describe the limits on what can evolve. The "phenotype set" is an assumption about what can evolve and to what extent; the "state equations" describe features of the situation that are assumed not to change. This distinction will become clearer when particular examples are discussed. Let us consider the three problems in turn.

SEX RATIO   For the sex ratio, the simplest assumption is that a parent can produce a fixed number N of offspring, and that the probability S that each birth will be a male can vary from parent to parent, over the complete range from 0 to 1; the phenotype set is then the set of values of S over this range. Fisher (28) extended this by supposing that males and females "cost" different amounts; i.e. he supposed

that a parent could produce α males and β females, where α and β are constrained to lie on or below the line $\alpha + \beta k = N$, and k is the cost of a female relative to that of a male. He then concluded that the parent should equalize expenditure on males and females. MacArthur (56) further broadened the phenotype set by insisting only that α and β lie on or below a line of arbitrary shape, and concluded that a parent should maximize $\alpha\beta$. A similar assumption was used by Charnov et al (11) to analyze the evolution of hermaphroditism as opposed to dioecy. Finally, it is possible to ask (97) what is the optimal strategy if a parent can choose not merely a value of S, and hence of the expected sex ratio, but also the variance of the sex ratio.

The important point in the present context is that the optimal solution depends on the assumption made. For example, Crow & Kimura (21) conclude that the sex ratio should be unity, but they do so for a model that assumes that $N = \alpha + \beta$ is a constant.

GAITS   In the analysis of gaits, it is assumed that the shapes of bones can vary, but the mechanical properties of bone, muscle and tendon cannot. It is also assumed that changes must be gradual; thus the gaits of ostrich, antelope and kangaroo are seen as different solutions to the same problem, not as solutions to different problems; i.e. they are different "adaptive peaks" (101).

FORAGING STRATEGY   In models of foraging behavior, a common assumption is that the way in which an animal allocates its time among various activities (e.g. consuming one prey item rather than another, searching in one kind of patch rather than another, moving between patches rather than continuing to search in the same one) can vary, but the efficiency with which it performs each act cannot. Thus, for example, the length of time it takes to "handle" (capture and consume) a given item, the time and energy spent in moving from place to place, and the time taken to find a given prey item at a given prey density are taken as invariant. Thus the models of foraging so far developed treat the phenotype set as the set of possible behavioral strategies, and treat structure and locomotory or perceptual skills as constants contributing to the state equations (which determine how rapidly an animal adopting some strategy acquires food). In principle there is no reason why optimization models should not be applied to the evolution of structure or skill also; it is simply a question of how the phenotype set is defined.

The Optimization Criterion

Some assumption must then be made concerning what quantity is being maximized. The most satisfactory is the inclusive fitness (see the section on Games Between Relatives, below); in many contexts the individual fitness (expected number of offspring) is equally good. Often, as in the second and third of my examples, neither criterion is possible, and some other assumption is needed. Two points must be made. First, the assumption about what is maximized is an assumption about what selective forces have been responsible for the trait; second, this assumption is part of the hypothesis being tested.

In most theories of sex ratio the basic assumption is that the ratio is determined by a gene acting in a parent, and what is maximized is the number of copies of that gene in future generations. The maximization has therefore a sound basis. Other maximization criteria have been used. For example, Kalmus & Smith (41) propose that the sex ratio maximizes the probability that two individuals meeting will be of different sexes; it is hard to understand such an eccentric choice when the natural one is available.

An equally natural choice—the maximization of the expected number of offspring produced in a lifetime—is available in theories of the evolution of life history strategies. But often no such easy choice is available.

In the analysis of gaits, Maynard Smith & Savage (66) assumed that the energy expenditure at a given speed would be minimized (or, equivalently, that the speed for a given energy expenditure was maximized). This led to the prediction that the proportion of time spent with all four legs off the ground should increase with speed and decrease with size.

In foraging theory, the common assumption is that the animal is maximizing its energy intake per unit time spent foraging. Schoener (87) points out that this is an appropriate choice, whether the animal has a fixed energy requirement and aims to minimize the time spent feeding so as to leave more time for other activities ("time minimizers"), or has a fixed time in which to feed during which it aims to maximize its energy gain ("energy maximizers"). There will, however, be situations in which this is not an appropriate choice. For example, there may be a higher risk of predation for some types of foraging than others. For some animals, the problem may not be to maximize energy intake per unit time, but to take in a required amount of energy, protein, etc, without taking an excess of any one of a number of toxins (S. A. Altmann, personal communication).

Pyke et al (81) point out that the optimal strategy depends on the time scale over which optimization is carried out, for two reasons. First, an animal that has sole access to some resource (e.g. a territory-holder) can afford to manage that resource so as to maximize its yield over a whole season. Second, and more general, optimal behavior depends on a knowledge of the environment, which can be acquired only by experience; this means that, in order to acquire information of value in the long run, an animal may have to behave in a way that is inefficient in the short run.

Having considered the phenotype set and the optimization criterion, a word must be said about their relationship to Levins' (51) concept of a fitness set. Levins was explicitly concerned with defining fitness "in such a way that interpopulation selection would be expected to change a species towards the optimum (maximum fitness) structure." This essentially group-selectionist approach led him to conclusions (e.g. for the conditions for a stable polymorphism) different from those reached from the classic analysis of gene frequencies (93). Nevertheless, Levins' attempt to unite ecological and genetic approaches did lead him to recognize the need for the concept of a fitness set, i.e. the set of all possible phenotypes, each phenotype being characterized by its (individual) fitness in each of the environments in which it might find itself.

Levins' fitness set is thus a combination of what I have called the phenotype set and of a measure of the fitness of each phenotype in every possible environment. It did not allow for the fact that fitnesses may be frequency-dependent (see the section on Games, below). The valuable insight in Levins' approach is that it is only possible to discuss what course phenotypic evolution may take if one makes explicit assumptions about the constraints on what phenotypes are possible. It may be better to use the term "phenotype set" to define these constraints, both because a description of possible phenotypes is a process prior to and separable from an estimation of their fitnesses, and because of the group-selectionist associations of the term "fitness set."

An Assumption About Heredity

Because natural selection cannot produce adaptation unless there is heredity, some assumption, explicit or otherwise, is always present. The nature of this assumption can be important. Fisher (28) assumed that the sex ratio was determined by autosomal genes expressed in the parent, and that mating was random. Hamilton (34) showed that the predicted optima are greatly changed if these assumptions are altered. In particular, he considered the effects of inbreeding, and of genes for meiotic drive. Rosado & Robertson (85), Trivers & Willard (96), and Trivers & Hare (95) have analyzed the effects of genes acting in the children and (in Hymenoptera) in the sterile castes.

It is unusual for the way in which a trait is inherited to have such a crucial effect. Thus in models of mammalian gaits no explicit assumption is made; the implicit assumption is merely that like begets like. The same is true of models of foraging, although in this case "heredity" can be cultural as well as genetic [e.g. (72), for feeding behavior of oyster-catchers].

The question of how optimization models can be tested is the main topic of the next three sections. A few preliminary remarks are needed. Clearly, the first requirement of a model is that the conclusions should follow from the assumptions. This seems not to be the case, for example, for Zahavi's (102) theory of sexual selection (61). A more usual difficulty is that the conclusions depend on unstated assumptions. For example, Fisher does not state that his sex ratio argument assumes random mating, and this was not noticed until Hamilton's 1967 paper (34). Maynard Smith & Price (65) do not state that the idea of an ESS (evolutionarily stable strategy) assumes asexual inheritance. It is probably true that no model ever states all its assumptions explicitly. One reason for writing this review is to encourage authors to become more aware of their assumptions.

A particular model can be tested either by a direct test of its assumptions, or by comparing its predictions with observation. The essential point is that in testing a model we are *not* testing the general proposition that nature optimizes, but the specific hypotheses about constraints, optimization criteria, and heredity. Usually we test whether we have correctly identified the selective forces responsible for the trait in question. But we should not forget hypotheses about constraints or heredity. For example, the weakest feature of theories concerning the sex ratio is that there is little evidence for the existence of genetic variance of the kind assumed by Fisher

[for references, see (63)]. It may be for this reason that the greatest successes of sex ratio theory (34, 95) have concerned Hymenoptera, in which it is easy to see how genes in the female parent can affect the sex of her children.

NEUTRALITY AND MALADAPTATION

I have said that when testing optimization models one is not testing the hypothesis that nature optimizes. But if it is not the case that the structure and behavior of organisms are nicely adapted to ensure their survival and reproduction, optimization models cannot be useful. What justification have we for assuming this?

The idea of adaptation is older than Darwinism. In the form of the argument from design it was a buttress of religious belief. For Darwin, the problem was not to prove that organisms were adapted but to explain how adaptation could arise without a creator. He was quite willing to accept that some characteristics are "selectively neutral." For example, he says (26) of the sterile dark red flower at the center of the umbel of the wild carrot: "That the modified central flower is of no functional importance to the plant is almost certain." Indeed, Darwin has been chided by Cain (8) for too readily accepting Owen's argument that the homology between bones of limbs of different vertebrates is nonadaptive. For Darwin the argument was welcome, because the resemblance could then be taken as evidence for genetic relationship (or, presumably, for a paucity of imagination on the part of the creator). But Cain points out that the homology would not have been preserved if it were not adaptive.

Biologists differ greatly in the extent to which they expect to find a detailed fit between structure and function. It may be symptomatic of the times that when, in conversation, I raised Darwin's example of the carrot, two different functional explanations were at once suggested. I suspect that these explanations were fanciful. But however much one may be in doubt about the function of the antlers of the Irish Elk or the tail of the peacock, one can hardly suppose them to be selectively neutral. In general, the structural and behavioral traits chosen for functional analysis are of a kind that rules out neutrality as a plausible explanation. Curio (23) makes the valid point that the ampullae of Lorenzini in elasmobranchs were studied for many years before their role in enabling a fish to locate prey buried in the mud was demonstrated (40), yet the one hypothesis that was never entertained was that the organ was functionless. The same could be said of Curio's own work (24) on the function of mobbing in birds; behavior so widespread, so constant, and so apparently dangerous calls for a functional explanation.

There are, however, exceptions to the rule that functional investigations are carried out with the aim of identifying particular selective forces, and not of demonstrating that traits are adaptive. The work initiated by Cain & Sheppard (9) on shell color and banding in *Cepaea* was in part aimed at refuting the claim that the variation was selectively neutral and explicable by genetic drift. To that extent, the work was aimed at demonstating adaptation as such; it is significant, however, that the work has been most successful when it has been possible to identify a particular selection pressure (e.g. predation by thrushes).

At present, of course, the major argument between neutral and selective theories concerns enzyme polymorphism. I cannot summarize the argument here, but a few points on methodology are relevant. The argument arose because of the formulation by Kimura (43) and King & Jukes (44) of the "neutral" hypothesis; one reason for proposing it was the difficulty of accounting for the extensive variation by selection. Hence the stimulus was quite different from that prompting most functional investigations; it was the existence of widespread variation in a trait of no obvious selective significance.

The neutral hypothesis is a good "Popperian" one; if it is false, it should be possible to show it. In contrast, the hypothesis of adaptation is virtually irrefutable. In practice, however, the statistical predictions of the neutral theory depend on so many unknowns (mutation rates, the past history of population number and structure, hitch-hiking from other loci) that it has proved hard to test (53). The difficulties have led some geneticists (e.g. 14) to propose that the only way in which the matter can be settled is by the classical methods of ecological genetics, i.e. by identifying the specific selection pressures associated with particular enzyme loci. The approach has had some success, but is always open to the objection that the loci for which the neutral hypothesis has been falsified are a small and biased sample.

In general, then, the problems raised by the neutral mutation theory and by optimization theory are wholly different. The latter is concerned with traits that differ between species and that can hardly be selectively neutral, but whose selective significance is not fully understood.

A more serious difficulty for optimization theory is the occurrence of maladaptive traits. Optimization is based on the assumption that the population is adapted to the contemporary environment, whereas evolution is a process of continuous change. Species lag behind a changing environment. This is particularly serious when studying species in an environment that has recently been drastically changed by man. For example, Lack (48) argued that the number of eggs laid by a bird maximizes the number of surviving young. Although there is much supporting evidence, there are some apparent exceptions. For example, the gannet *Sula bassana* lays a single egg. Studying gannets on the Bass Rock, Nelson (71) found that if a second egg is added the pair can successfully raise two young. The explanation can hardly be a lack of genetic variability, because species nesting in the Humboldt current off Peru lay and successfully raise two or even three eggs.

Lack (48) suggests that the environment for gannets may recently have improved, as evidenced by the recent increase in the population on the Bass Rock. Support for this interpretation comes from the work of Jarvis (39) on the closely related *S. capensis* in South Africa. This species typically lays one egg, but 1% of nests contain two. Using methods similar to Nelson's, Jarvis found that a pair can raise two chicks to fledgings, but that the average weight of twins was lower than singles, and in each nest one twin was always considerably lighter than its fellow. There is good evidence that birds fledging below the average weight are more likely to die soon after. Difficulties of a similar kind arise for the Glaucous Gull (see 45).

The undoubted existence of maladaptive traits, arising because evolutionary change is not instantaneous, is the most serious obstacle to the testing of optimiza-

tion theories. The difficulty must arise; if species were perfectly adapted evolution would cease. There is no easy way out. Clearly a wholesale reliance on evolutionary lag to save hypotheses that would otherwise be falsified would be fatal to the whole research program. The best we can do is to invoke evolutionary lag sparingly, and only when there are independent grounds for believing that the environment has changed recently in a relevant way.

What then is the status of the concept of adaptation? In the strong form—that all organs are perfectly adapted—it is clearly false; the vermiform appendix is sufficient to refute it. For Darwin, adaptation was an obvious fact that required an explanation; this still seems a sensible point of view. Adaptation can also be seen as a necessary consequence of natural selection. The latter I regard as a refutable scientific theory (60); but it must be refuted, if at all, by genetic experiment and not by the observation of complex behavior.

CRITIQUES OF OPTIMIZATION THEORY

Lewontin (55) raises a number of criticisms, which I discuss in turn.

Do Organs Solve Problems?

Most organs have many functions. Therefore, if a hypothesis concerning function fails correctly to predict behavior, it can always be saved by proposing an additional function. Thus hypotheses become irrefutable and metaphysical, and the whole program merely a test of ingenuity in conceiving possible functions. Three examples follow; the first is one used by Lewontin.

Orians & Pearson (73) calculated the optimal food item size for a bird, on the assumption that food intake is to be maximized. They found that the items diverged from random in the expected direction, but did not fit the prediction quantitatively. They explained the discrepancy by saying that a bird must visit its nest frequently to discourage predators. Lewontin (54) comments:

> This is a paradigm for adaptive reconstruction. The problem is originally posed as efficiency for food-gathering. A deviation of behavior from random, in the direction predicted, is regarded as strong support for the adaptive explanation of the behavior and the discrepancy from the predicted optimum is accounted for by an ad hoc secondary problem which acts as a constraint on the solution to the first. . . . By allowing the theorist to postulate various combinations of "problems" to which manifest traits are optimal "solutions", the adaptationist programme makes of adaptation a metaphysical postulate, not only incapable of refutation, but necessarily confirmed by every observation. This is the caricature that was immanent in Darwin's insight that evolution is the product of natural selection.

It would be unfair to subject Orians alone to such criticism, so I offer two further examples from my own work.

First, as explained earlier, Maynard Smith & Savage (66) predicted qualitative features of mammalian gaits. However, their model failed to give a correct quantitative prediction. I suspect that if the model were modified to allow for wind resistance and the visco-elastic properties of muscle, the quantitative fit would be improved;

at present, however, this is pure speculation. In fact, it looks as if a model that gives quantitatively precise predictions will be hard to devise (1).

Second, Maynard Smith & Parker (64) predicted that populations will vary in persistence or aggressiveness in contest situations, but that individuals will not indicate their future behavior by varying levels of intensity of display. Rohwer (84) describes the expected variability in aggressivity in the Harris sparrow in winter flocks, but also finds a close correlation between aggressivity and a signal (amount of black in the plumage). I could point to the first observation as a confirmation of our theory, and explain how, by altering the model (by changing the phenotype set to permit the detection of cheating), one can explain the second.

What these examples, and many others, have in common is that a model gives predictions that are in part confirmed by observation but that are contradicted in some important respect. I agree with Lewontin that such discrepancies are inevitable if a simple model is used, particularly a model that assumes each organ or behavior to serve only one function. I also agree that if the investigator adds assumptions to his model to meet each discrepancy, there is no way in which the hypothesis of adaptation can be refuted. But the hypothesis of adaptation is not under test.

What is under test is the specific set of hypotheses in the particular model. Each of the three example models above has been falsified, at least as a complete explanation of these particular data. But since all have had some qualitative success, it seems quite appropriate to modify them (e.g. by allowing for predation, for wind resistance, for detection of cheating). What is not justified is to modify the model and at the same time to claim that the model is confirmed by observation. For example, Orians would have to show that his original model fits more closely in species less exposed to predation. I would have to show that Rohwer's data fit the "mixed ESS" model in other ways—in particular, that the fitness of the different morphs are approximately equal. If, as may well be the case, the latter prediction of the ESS model does not hold, it is hard to see how it could be saved.

If the ESS model proves irrelevant to the Harris sparrow, it does not follow, however, that it is never relevant. By analogy, the assertion is logically correct that there will be a stable polymorphism if the heterozygote at a locus with two alleles is fitter than either homozygote. The fact that there are polymorphisms not maintained by heterosis does not invalidate the logic. The (difficult) empirical question is whether polymorphisms are often maintained by heterosis. I claim a similar logical status for the prediction of a mixed ESS.

In population biology we need simple models that make predictions that hold qualitatively in a number of cases, even if they are contradicted in detail in all of them. One can say with some confidence, for example, that no model in May's *Stability and Complexity in Model Ecosystems* describes exactly any actual case, because no model could ever include all relevant features. Yet the models do make qualitative predictions that help to explain real ecosystems. In the analysis of complex systems, the best we can hope for are models that capture some essential feature.

To summarize my comments on this point, Lewontin is undoubtedly right to complain if an optimizer first explains the discrepancy between theory and observation by introducing a new hypothesis, and then claims that his modified theory has

been confirmed. I think he is mistaken in supposing that the aim of optimization theories is to confirm a general concept of adaptation.

Is There Genetic Variance?

Natural selection can optimize only if there is appropriate genetic variance. What justification is there for assuming the existence of such variance? The main justification is that, with rare exceptions, artificial selection has always proved effective, whatever the organism or the selected character (53).

A particular difficulty arises because genes have pleiotropic effects, so that selection for trait A may alter trait B; in such cases, any attempt to explain the changes in B in functional terms is doomed to failure. There are good empirical grounds for doubting whether the difficulty is as serious as might be expected from the widespread nature of pleiotropy. The point can best be illustrated by a particular example. Lewontin (54) noted that in primates there is a constant allometric relationship between tooth size and body size. It would be a waste of time, therefore, to seek a functional explanation of the difference between the tooth size of the gorilla and of the rhesus monkey, since the difference is probably a simple consequence of the difference in body size.

It is quite true that for most teeth there is a constant allometric relationship between tooth and body size, but there is more to it than that (36). The canine teeth (and the teeth occluding with them) of male primates are often larger than those of females, even when allowance has been made for the difference in body size. This sex difference is greater in species in which males compete for females than in monogamous species, and greater in ground-living species (which are more exposed to predation) than in arboreal ones. Hence there is sex-limited genetic variance for canine tooth size, independent of body size, and the behavioral and ecological correlations suggest that this variance has been the basis of adaptation. It would be odd if there were tooth-specific, sex-limited variance, but no variance for the relative size of the teeth as a whole. However, there is some evidence for the latter. The size of the cheek teeth in females (relative to the size predicted from their body size) is significantly greater in those species with a higher proportion of leaves (as opposed to fruit, flowers, or animal matter) in their diets.

Thus, although at first sight the data on primate teeth suggest that there may be nothing to explain in functional terms, a more detailed analysis presents quite a different picture. More generally, changes in allometric relationships can and do occur during evolution (30).

I have quoted Lewontin as a critic of adaptive explanation, but it would misinterpret him to imply that he rejects all such explanations. He remarks (54) that "the serious methodological difficulties in the use of adaptive arguments should not blind us to the fact that many features of organisms are adaptations to obvious environmental 'problems.'" He goes on to argue that if natural selection is to produce adaptation, the mapping of character states into fitnesses must have two characteristics: "continuity" and "quasi-independence." By continuity is meant that small changes in a character result in small changes in the ecological relations of the organism; if this were not so it would be hard to improve a character for one role

without ruining it for another. By quasi-independence is meant that the developmental paths are such that a variety of mutations may occur, all with the same effect on the primary character, but with different effects on other characters. It is hard to think of better evidence for quasi-independence than the evolution of primate canines.

To sum up this point, I accept the logic of Lewontin's argument. If I differ from him (and on this point he is his own strongest critic), it is in thinking that genetic variance of an appropriate kind will usually exist. But it may not always do so.

It has been an implicit assumption of optimization models that the optimal phenotype can breed true. There are two kinds of reasons why this might not be true. The first is that the optimal phenotype may be produced by a heterozygote. This would be a serious difficulty if one attempted to use optimization methods to analyze the genetic structure of populations, but I think that would be an inappropriate use of the method. Optimization models are useful for analyzing phenotypic evolution, but not the genetic structuring of populations. A second reason why the optimal phenotype may not breed true is more serious: the evolutionarily stable population may be phenotypically variable. This point is discussed further in the section on Games, below.

The assumption concerning the phenotype set is based on the range of variation observable within species, the phenotypes of related species, and on plausible guesses at what phenotypes might arise under selection. It is rare to have any information on the genetic basis of the phenotypic variability. Hence, although it is possible to introduce specific genetic assumptions into optimization models (e.g. 2, 89), this greatly complicates the analysis. In general, the assumption of "breeding true" is reasonable in particular applications; models in which genes appear explicitly need to be analyzed to decide in what situations the assumption may mislead us.

The Effects of History

If, as Wright (101) suggested, there are different "adaptive peaks" in the genetic landscape, then depending on initial conditions, different populations faced with identical "problems" may finish up in different stable states. Such divergence may be exaggerated if evolution takes the form of a "game" in which the optimal phenotype for one individual depends on what others are doing (see the section on Games, below). An example is Fisher's (28) theory of sexual selection, which can lead to an "auto-catalytic" exaggeration of initially small differences. Jacob (38) has recently emphasized the importance of such historical accidents in evolution.

As an example of the difficulties that historical factors can raise for functional explanations, consider the evolution of parental care. A simple game-theory model (62) predicts that for a range of ecological parameters either of two patterns would be stable: male parental care only, or female care only. Many fish and amphibia show one or the other of these patterns. At first sight, the explanation of why some species show one pattern and others the other seems historical; the reasons seem lost in an unknown past. However, things may not be quite so bad. At a recent discussion of fish behavior at See-Wiesen the suggestion emerged that if uniparental care evolved from no parental care, it would be male care, whereas if it evolved from biparental

care it would be female care. This prediction is plausible in the light of the original game-theory model, although not a necessary consequence of it. It is, however, testable by use of the comparative data; if it is true, male care should occur in families that also include species showing no care, and female care in families that include species showing biparental care. This may not prove to be the case; the example is given to show that even if there are alternative adaptive peaks, and in the absence of a relevant fossil record, it may still be possible to formulate testable hypotheses.

What Optimization Criterion Should One Use?

Suppose that, despite all difficulties, one has correctly identified the "problem." Suppose, for example, that in foraging it is indeed true that an animal should maximize E, its rate of energy intake. We must still decide in what circumstances to maximize E. If the animal is alone in a uniform environment, no difficulty arises. But if we allow for competition and for a changing environment, several choices of optimization procedure are possible. For example, three possibilities arise if we allow just for competition:

1. The "maximin" solution: Each animal maximizes E on the assumption that other individuals behave in the least favorable way for it.
2. The "Pareto" point: The members of the population behave so that no individual can improve its intake without harming others.
3. The ESS: The members of the population adopt feeding strategy I such that no mutant individual adopting a strategy other than I could do better than typical members.

These alternatives are discussed further in the section on Games, below. For the moment, it is sufficient to say that the choice among them is not arbitrary, but follows from assumptions about the mode of inheritance and the population structure. For individual selection and parthenogenetic inheritance, the ESS is the appropriate choice.

Lewontin's criticism would be valid if optimizers were in the habit of assuming the truth of what Haldane once called "Pangloss' theorem," which asserts that animals do those things that maximize the chance of survival of their species. If optimization rested on Pangloss' theorem it would be right to reject it. My reason for thinking that Lewontin regards optimization and Pangloss' theorem as equivalent is that he devotes the last section of his paper to showing that in *Drosophila* a characteristic may be established by individual selection and yet may reduce the competitive ability of the population relative to others. The point is correct and important, but in my view does not invalidate most recent applications of optimization.

THE METHODOLOGY OF TESTING

The crucial hypothesis under test is usually that the model correctly incorporates the selective forces responsible for the evolution of a trait. Optimization models

sometimes make fairly precise quantitative predictions that can be tested. However, I shall discuss the question of how functional explanations can be tested more generally, including cases in which the predictions are only qualitative. It is convenient to distinguish comparative, quantitative, and individual-variation methods.

Comparative Tests

Given a functional hypothesis, there are usually testable predictions about the development of the trait in different species. For example, two main hypothesis have been proposed to account for the greater size of males in many mammalian species: It is a consequence of competition among males for females; or it arises because the two sexes use different resources. If the former hypothesis is true, dimorphism should be greater in harem-holding and group-living species, whereas if the latter is true it should be greater in monogamous ones, and in those with a relatively equal adult sex ratio.

Clutton-Brock et al (16) have tested these hypotheses by analyzing 42 species of primates (out of some 200 extant species) for which adequate breeding data are available. The data are consistent with the sexual selection hypothesis, and show no sign of the trend predicted by the resource differentiation hypothesis. The latter can therefore be rejected, at least as a major cause of sexual dimorphism in primates. It does not follow that inter-male competition is the only relevant selective factor (82). Nor do their observations say anything about the causes of sexual dimorphism in other groups. It is interesting (though not strictly relevant at this point) that the analysis also showed a strong correlation between female body size and degree of dimorphism. This trend, as was first noted by Rensch (83), occurs in a number of taxa, but has never received an entirely satisfactory explanation.

The comparative method requires some criterion for inclusion of species. This may be purely taxonomic (e.g. all primates, all passerine birds), or jointly taxonomic and geographic (e.g. all African ungulates, all passerines in a particular forest). Usually, some species must be omitted because data are not available. Studies on primates can include a substantial proportion of extant species (16, 68); in contrast, Schoener (86), in one of the earliest studies of this type, included all birds for which data were available and that also met certain criteria of territoriality, but he had to be content with a small fraction of extant species. It is therefore important to ask whether the sample of species is biased in ways likely to affect the hypothesis under test. Most important is that there be some criterion of inclusion, since otherwise species may be included simply because they confirm (or contradict) the hypothesis under test.

Most often, limitations of data will make it necessary to impose both taxonomic and geographic criteria. This need not prevent such data from being valuable, either in generating or in testing hypotheses; examples are analyses of flocking in birds (7, 31) and of breeding systems in forest plants (3, 4).

A second kind of difficulty concerns the design of significance tests. Different species cannot always be treated as statistically independent. For example, all gibbons are monogamous, and all are arboreal and frugivorous, but, since all may be descended from a single ancestor with these properties, they should be treated as

a single case in any test of association (not that any is suspected). To take an actual example of this difficulty, Lack (49) criticized Verner & Willson's (98) conclusion that polygamy in passerines is associated with marsh and prairie habitats on the grounds that many of the species concerned belong to a single family, the Icteridae.

Statistical independence and other methodological problems in analyzing comparative data are discussed by Clutton-Brock & Harvey (17). In analyzing the primate data, they group together as a single observation all congeneric species belonging to the same ecological category. This is a conservative procedure, in that it is unlikely to find spurious cases of statistical significance. Their justification for treating genera, but not families, as units is that for their data there are significant differences between genera within families for seven of the eight ecological and behavioral variables, but significant additional variation between families for only two of them. It may be, however, that a more useful application of statistical methods is their use (17) of partial regression, which enables them to examine the effects of a particular variable when the effects of other variables have been removed, and to ask how much of the total variation in some trait is accounted for by particular variables.

Quantitative Tests

Quantitative tests can be illustrated by reference to some of the predictions of foraging theory. Consider first the problem of optimal diet. The following model situation has been widely assumed. There are a number of different kinds of food items. An animal can search simultaneously for all of them. Each item has a characteristic food value and "handling time" (the time taken to capture and consume it). For any given set of densities and hence frequencies of encounter, the animal must only decide which items it should consume and which ignore.

Pyke et al (81) remark that no fewer than eight authors have independently derived the following basic result. The animal should rank the items in order of $V =$ food value/handling time. Items should be added to the diet in rank order, provided that for each new item the value of V is greater than the rate of food intake for the diet without the addition. This basic result leads to three predictions:

1. Greater food abundance should lead to greater specialization. This qualitative prediction was first demonstrated by Ivlev (37) for various fish species in the laboratory, and data supporting it have been reviewed by Schoener (87). Curio (25) quotes a number of cases that do not fit.
2. For fixed densities, a food type should either be always taken, or never taken.
3. Whether a food item should be taken is independent of its density, and depends on the densities of food items of higher rank.

Werner & Hall (100) allowed bluegill sunfish to feed on *Daphnia* of three different size classes; the diets observed agreed well with the predictions of the model. Krebs et al (47) studied Great Tits foraging for parts of mealworms on a moving conveyor belt. They confirmed prediction 3 but not 2; that is, they found that whether small pieces were taken was independent of the density of small pieces, but, as food abundance rose, small pieces were dropped only gradually from the diet. Goss-

Custard (29) has provided field evidence confirming the model from a study of redshank feeding on marine worms of different sizes, and Pulliam (80) has confirmed it for Chipping Sparrows feeding on seeds.

Turning to the problem of how long an animal should stay in a patch before moving to another, there is again a simple prediction, which Charnov (10) has called the "Marginal Value Theorem" [the same theorem was derived independently by Parker & Stuart (77) in a different context]. It asserts that an animal should leave a patch when its rate of intake in the patch (its "marginal" rate) drops to the average rate of intake for the habitat as a whole. It is a corollary that the marginal rate should be the same for all patches in the habitat. Two laboratory experiments on tits (20, 46) agree well with the prediction.

A more general problem raised by these experiments is discussed by Pyke et al (81). How does an animal estimate the parameters it needs to know before it can perform the required optimization? How much time should it spend acquiring information? Sometimes these questions may receive a simple answer. Thus the results of Krebs et al (46) suggest that a bird leaves a patch if it has not found an item of food for some fixed period τ (which varied with the overall abundance of food). The bird seems to be using τ, or rather $1/\tau$, as an estimate of its marginal capture rate. But not all cases are so simple.

Individual Variation

The most direct way of testing a hypothesis about adaptation is to compare individuals with different phenotypes, to see whether their fitnesses vary in the way predicted by the hypothesis. This was the basis of Kettlewell's (42) classic demonstration of selection on industrial melanism in moths. In principle, the individual differences may be produced by experimental interference [Curio's (23) "method of altering a character"] or they may be genetic or of unknown origin (Curio's "method of variants"). Genetic differences are open to the objection that genes have pleiotropic effects, and occasionally are components of supergenes in which several closely linked loci affecting the same function are held in linkage disequilibrium, so that the phenotypic difference responsible for the change in fitness may not be the one on which attention is concentrated. This difficulty, however, is trivial compared to that which arises when two species are compared.

The real difficulty in applying this method to behavioral differences is that suitable individual differences are often absent and experimental interference is impractical. Although it is hard to alter behavior experimentally, it may be possible to alter its consequences. Tinbergen et al (94) tested the idea that gulls remove egg shells from the nest because the shells attract predators to their eggs and young; they placed egg shells close to eggs and recorded a higher predation rate.

However, the most obvious field of application of this method arises when a population is naturally variable. Natural variation in a phenotype may be maintained by frequency-dependent selection; in game-theoretical terms, the stable state may be a mixed strategy. If a particular case of phenotypic variability (genetic or not) is thought to be maintained in this way, it is important to measure the fitnesses of individuals with different phenotypes. At a mixed ESS (which assumes partheno-

genetic inheritance) these fitnesses are equal; with sexual reproduction, exact equality is not guaranteed, but approximate equality is a reasonable expectation (91). If the differences are not genetic, we still expect a genotype to evolve that adopts the different strategies with frequencies that equalize their payoffs.

The only test of this kind known to me is Parker's (76) measurement of the mating success of male dungflies adopting different strategies. His results are consistent with a "mixed ESS" interpretation; it is not known whether the differences are genetic. The importance of tests of this kind lies in the fact that phenotypic variability can have other explanations; for example, it may arise from random environmental effects, or from genes with heterotic effects. In such cases, equality of fitness between phenotypes is not expected.

MATHEMATICAL APPROACHES TO OPTIMIZATION

During the past twenty years there has been a rapid development of mathematical techniques aimed at solving problems of optimization and control arising in economics and engineering. These stem from the concepts of "dynamic programming" (5) and of the "maximum principle" (79). The former is essentially a computer procedure to seek the best control policy in particular cases without the hopelessly time-consuming task of looking at every possibility. The latter is an extension of the classic methods of the calculus of variations that permits one to allow for "inequality" constraints on the state and control variables (e.g. in the resource allocation model discussed below, the proportion u of the available resources allocated to seeds must obey the constraint $u < 1$).

This is not the place to describe these methods, even if I were competent to do so. Instead, I shall describe the kinds of problems that can be attacked. If a biologist has a problem of one of these kinds, he would do best to consult a mathematician. For anyone wishing to learn more of the mathematical background, Clark (12) provides an excellent introduction.

I discuss in turn "optimization," in which the problem is to choose an optimal policy in an environment without competitors; "games," in which the environment includes other "players" who are also attempting to optimize something; and "games of inclusive fitness," in which the "players" have genes in common. I shall use as an illustration the allocation of resources between growth and reproduction.

Optimization

CHOICE OF A SINGLE VALUE   The simplest type of problem, which requires for its solution only the technique of differentiation, is the choice of a value for a single parameter. For example, in discussing the evolution of gaits, Maynard Smith & Savage (66) found an expression for P, the power output, as a function of the speed V, of size S, and of J, the fraction of time for which all four legs are off the ground. By solving the equation $dP/dJ = 0$, an equation $J = f(V,S)$ was obtained, describing the optimum gait as a function of speed and size.

Few problems are as simple as this, but some more complex cases can be reduced to problems of this kind, as will appear below.

A SIMPLE PROBLEM IN SEQUENTIAL CONTROL   Most optimization theory is concerned with how a series of sequential decisions should be taken. For example, consider the growth of an annual plant (19, 69). The rate at which the plant can accumulate resources depends on its size. The resources can be allocated either for further growth, or to seeds, or divided between them. For a fixed starting size and length of season, how should the plant allocate its resources so as to maximize the total number of seeds produced?

In this problem, the "state" of the system at any time is given simply by the plant's size, x; the "control variable" $u(t)$ is the fraction of the incoming resource allocated to seeds at time t; the "constraints" are the initial size, the length of the season, the fact that $u(t)$ must lie between 0 and 1, and the "state equation,"

$$dx/dt = F[x(t), u(t)], \qquad\qquad 1.$$

which describes how the system changes as a function of its state and of the control variable.

If equation 1 is linear in u, it can be shown that the optimal control is "bang-bang"—that is, $u(t) = 0$ up to some critical time t^*, and subsequently $u(t) = 1$. The problem is thus reduced to finding the single value, t^*. But if equation 1 is nonlinear, or has stochastic elements, the optimal control may be graded.

MORE COMPLEX CONTROL PROBLEMS   Consider first the "state" of the system. This may require description by a vector rather than by a single variable. Thus suppose the plant could also allocate resources to the production of toxins that increased its chance of survival. Then its state would require measures of both size and toxicity. The state description must be sufficient for the production of a state equation analogous to equation 1. The state must also include any information used in determining the control function $u(t)$. This is particularly important when analyzing the behavior of an animal that can learn. Thus suppose that an animal is foraging, and that its decisions on whether to stay in a given patch or to move depend on information it has acquired about the distribution of food in patches; then this information is part of the state of the animal [for a discussion, see (20)].

Just as the state description may be multi-dimensional, so may the control function; for example, for the toxic plant the control function must specify the allocation both to seeds and to toxins.

The state equation may be stochastic. Thus the growth of a plant depends on whether it rains. A plant may be supposed to "know" the probability of rain (i.e. its genotype may be adapted to the frequency of rain in previous generations) but not whether it will actually rain. In this case, a stochastic state equation may require a graded control. This connection between stochasticity and a "compromise" response as opposed to an all-or-none one is a common feature of optimal control. A second example is the analysis by Oster & Wilson (75) of the optimal division into castes in social insects: A predictable environment is likely to call for a single type of worker, while an uncertain one probably calls for a division into several castes.

REVERSE OPTIMALITY   McFarland (67) has suggested an alternative approach. The typical one is to ask how an organism should behave in order to maximize its fitness. Mathematically, this requires that one define an "objective function" that must be maximized ("objective" here means "aim" or "goal"); in the plant example, the objective function is the number of seeds produced, expressed as a function of x and $u(t)$. But a biologist may be faced with a different problem. Suppose that he knew, by experiment, how the plant actually allocates its resources. He could then ask what the plant is actually maximizing. If the plant is perfectly adapted, the objective function so obtained should correspond to what Sibly & McFarland (88) call the "cost function"—i.e. the function that should be maximized if the organism is maximizing its fitness. A discrepancy would indicate maladaptation.

There are difficulties in seeing how this process of reverse optimality can be used. Given that the organism's behavior is "consistent" (i.e. if it prefers A to B and B to C, it prefers A to C), it is certain that its behavior maximizes *some* objective function; in general there will be a set of functions maximized. Perfect adaptation then requires only that the cost function correspond to one member of this set. A more serious difficulty is that it is not clear what question is being asked. If a discrepancy is found, it would be hard to say whether this was because costs had been wrongly measured or because the organism was maladapted. This is a particular example of my general point that it is not sensible to test the hypothesis that animals optimize. But it may be that the reverse optimality approach will help to analyze how animals in fact take decisions.

Games

Optimization of the kind just discussed treats the environment as fixed, or as having fixed stochastic properties. It corresponds to that part of population genetics that assumes fitnesses to be independent of genotype frequencies. A number of selective processes have been proposed as frequency-dependent, including predation (13, 70) and disease (15, 32). The maintenance of polymorphism in a varied environment (50) is also best seen as a case of frequency-dependence (59). The concept can be applied directly to phenotypes.

The problem is best formulated in terms of the theory of games, first developed (99) to analyze human conflicts. The essence of a game is that the best strategy to adopt depends on what one's opponent will do; in the context of evolution, this means that the fitness of a phenotype depends on what others are present; i.e. fitnesses are frequency-dependent.

The essential concepts are those of a "strategy" and a "payoff matrix." A strategy is a specification of what a "player" will do in every situation in which it may find itself; in the plant example, a typical strategy would be to allocate all resources to growth for 20 days, and then divide resources equally between growth and seeds. A strategy may be "pure" (i.e. without chance elements) or "mixed" (i.e. of the form "do A with probability p and B with probability $1-p$," where A and B are pure strategies).

The "payoff" to an individual adopting strategy A in competition to one adopting B is written $E(A, B)$, which expresses the expected *change* in the fitness of the player

adopting A if his opponent adopts B. The evolutionary model is then of a population of individuals adopting different strategies. They pair off at random, and their fitnesses change according to the payoff matrix. Each individual then produces offspring identical to itself, in numbers proportional to the payoff it has accumulated. Inheritance is thus parthenogenetic, and selection acts on the individual. It is also assumed that the population is infinite, so that the chance of meeting an opponent adopting a particular strategy is independent of one's own strategy.

The population will evolve to an evolutionarily stable strategy, or ESS, if one exists (64). An ESS is a strategy that, if almost all individuals adopt it, no rare mutant can invade. Thus let I be an ESS, and J a rare mutant strategy of frequency $p \ll 1$. Writing the fitnesses of I and J as $W(I)$ and $W(J)$,

$$W(I) = C + (1-p) \, E \, (I, \, I) + p \, E \, (I, \, J);$$

$$W(J) = C + (1-p) \, E \, (J, \, I) + p \, E \, (J, \, J).$$

In these equations C is the fitness of an individual before engaging in a contest. Since I is an ESS, $W(I) > W(J)$ for all $J \neq I$; that is, remembering that p is small, *either*

$$E \, (I, \, I) > E \, (J, \, I), \text{ or}$$

$$E \, (I, \, I) = E \, (J, \, I) \text{ and } E \, (I, \, J) > E \, (J, \, J). \qquad 2.$$

These conditions (expressions 2) are the definition of an ESS.

Consider the matrix in Table 1. For readers who prefer a biological interpretation, A is "Hawk" and B is "Dove"; thus A is a bad strategy to adopt against A, because of the risk of serious injury, but a good strategy to adopt against B, and so on.

The game has no pure ESS, because $E \, (A, \, A) < E \, (B, \, A)$ and $E \, (B, \, B) < E \, (A, \, B)$. It is easy to show that the mixed strategy—playing A and B with equal probability—is an ESS. It is useful to compare this with other "solutions," each of which has a possible biological interpretation:

THE MAXIMIN SOLUTION   This is the pessimist's solution, playing the strategy that minimizes your losses if your opponent does what is worst for you. For our matrix, the maximin strategy is always to play B. Lewontin (52) suggested that this strategy is appropriate if the "player" is a species and its opponent nature: The species should minimize its chance of extinction when nature does its worst. This is the "existential game" of Slobodkin & Rapoport (92). It is hard to see how a

Table 1 Payoff matrix for a game; the values in the matrix give the payoff to Player 1

	Player 2	
	A	B
Player 1		
A	1	5
B	2	4

species could evolve this strategy, except by group selection. (Note that individual selection will not necessarily minimize the chance of death: A mutant that doubled the chance that an individual would die before maturity, but that quadrupled its fecundity if it did survive, would increase in frequency.)

THE NASH EQUILIBRIUM   This is a pair of strategies, one for each player, such that neither would be tempted to change his strategy so long as the other continues with his. If in our matrix, player 1 plays A and 2 plays B, we have a Nash equilibrium; this is also the case if 1 plays B and 2 Plays A. A population can evolve to the Nash point if it is divided into two classes, and if members of one class compete only with members of the other. Hence it is the appropriate equilibrium in the "parental investment" game (62), in which all contests are between a male and a female. The ESS is subject to the added constraint that both players must adopt the same strategy.

THE GROUP SELECTION EQUILIBRIUM   If the two players have the same genotype, genes in either will be favored that maximize the sum of their payoffs. For our matrix both must play strategy B. The problem of the stable strategy when the players are related but not identical is discussed in the section on Games Between Relatives, below.

It is possible to combine the game-theoretical and optimization approaches. Mirmirani & Oster (69) make this extension in their model of resource allocation in plants. They ask two questions. What is the ESS for a plant growing in competition with members of its own species? What is the ESS when two species compete with one another?

Thus consider two competing plants whose sizes at time t are P_1 and P_2. The effects of competition are allowed for by writing

$$dP_1/dt = (r_1 - e_1P_2)(1 - u_1)P_1,$$
$$dP_2/dt = (r_2 - e_2P_1)(1 - u_2)P_2,$$

3.

where u_1 and u_2 are the fractions of the available resources allocated to seeds. Let $J_1[u_1(t), u_2(t)]$ be the total seed production of plant 1 if it adopts the allocation strategy $u_1(t)$ and its competitor adopts $u_2(t)$. Mirmirani & Oster seek a stable pair of strategies $u_1^*(t)$, $u_2^*(t)$, such that

$$J_1[u_1(t), u_2^*(t)] \leqslant J_1[u_1^*(t), u_2^*(t)], \text{ and}$$
$$J_2[u_1^*(t), u_2(t)] \leqslant J_2[u_1^*(t), u_2^*(t)].$$

4.

That is, they seek a Nash equilibrium, such that neither competitor could benefit by unilaterally altering its strategy. They find that the optimal strategies are again "bang-bang," but with earlier switching times than in the absence of competition. Strictly, the conditions indicated by expressions 4 are correct only when there is competition between species, and when individuals of one species compete only with individuals of the other; formally this would be so if the plants grew alternately in

a linear array. The conditions indicated by expressions 4 are not appropriate for intra-specific competition, since they permit $u_1^*(t)$ and $u_2^*(t)$ to be different, which could not be the case unless individuals of one genotype competed only with individuals of the other. For intra-specific competition ($r_1 = r_2$, $e_1 = e_2$), the ESS is given by

$$J_1[u_1(t), u_1^*(t)] \leqslant J_1[u_1^*(t), u_1^*(t)]. \qquad 5.$$

As it happens, for the plant growth example equations 4 and 5 give the same control function, but in general this need not be so.

The ESS model assumes parthenogenetic inheritance, whereas most interesting populations are sexual. If the ESS is a pure strategy, no difficulty arises; a genetically homgeneous sexual population adopting the strategy will also be stable. If the ESS is a mixed strategy that can be achieved by a single individual with a variable behavior, there is again no difficulty. If the ESS is a mixed one that can only be achieved by a population of pure strategists in the appropriate frequencies, two difficulties arise:

1. Even with the parthenogenetic model, the conditions expressed in expressions 2 do not guarantee stability. (This was first pointed out to me by Dr. C. Strobeck.) In such cases, therefore, it is best to check the stability of the equilibrium, if necessary by simulation; so far, experience suggests that stability, although not guaranteed, will usually be found.
2. The frequency distribution may be one that is incompatible with the genetic mechanism. This difficulty, first pointed out by Lewontin (52), has recently been investigated by Slatkin (89–91) and by Auslander et al (2). It is hard to say at present how serious it will prove to be; my hope is that a sexual population will usually evolve a frequency distribution as close to the ESS as its genetic mechanism will allow.

Games Between Relatives

The central concept is that of "inclusive fitness" (33). In classical population genetics we ascribe to a genotype I a "fitness" W_i, corresponding to the expected number of offspring produced by I. If, averaged over environments and genetic backgrounds, the effect of substituting allele A for a is to increase W, allele A will increase in frequency. Following Oster et al (74), but ignoring unequal sex ratios, Hamilton's proposal is that we should replace W_i by the inclusive fitness, Z_i, where

$$Z_i = \sum_{j=1}^{R} r_{ij} W_j, \qquad 6.$$

where the summation is over all R relatives of I; r_{ij} is the fraction of J's genome that is identical by descent to alleles in I; and W_j is the expected number of offspring of the jth relative of I. (If $J = I$, then equation 6 refers to the component of inclusive fitness from an individual's own offspring.)

An allelle A will increase in frequency if it increases Z, rather than just W. Three warnings are needed:

1. It is usual to calculate r_{ij} from the pedigree connecting I and J [as carried out, for example, by Malecot (58)]. However, if selection is occurring, r_{ij} so estimated is only approximate, as are predictions based on equation 6 (35).
2. Some difficulties arose in calculating appropriate values of r_{ij} for haplo-diploids; these were resolved by Crozier (22).
3. If the sex ratio is not unity, additional difficulties arise (74).

Mirmirani & Oster (69) have extended their plant-growth model along these lines to cover the case when the two competitors are genetically related. They show that as r increases, the switching time becomes earlier and the total yield higher.

CONCLUSION

The role of optimization theories in biology is not to demonstrate that organisms optimize. Rather, they are an attempt to understand the diversity of life.

Three sets of assumptions underlie an optimization model. First, there is an assumption about the kinds of phenotypes or strategies possible (i.e. a "phenotype set"). Second, there is an assumption about what is being maximized; ideally this should be the inclusive fitness of the individual, but often one must be satisfied with some component of fitness (e.g. rate of energy intake while foraging). Finally, there is an assumption, often tacit, about the mode of inheritance and the population structure; this will determine the type of equilibrium to which the population will move.

In testing an optimization model, one is testing the adequacy of these hypotheses to account for the evolution of the particular structures or patterns of behavior under study. In most cases the hypothesis that variation in the relevant phenotypes is selectively neutral is not a plausible alternative, because of the nature of the phenotypes chosen for study. However, it is often a plausible alternative that the phenotypes are not well adapted to current circumstances because the population is lagging behind a changing environment; this is a serious difficulty in testing optimization theories.

The most damaging criticism of optimization theories is that they are untestable. There is a real danger that the search for functional explanations in biology will degenerate into a test of ingenuity. An important task, therefore, is the development of an adequate methodology of testing. In many cases the comparative method is the most powerful; it is, however, essential to have clear criteria for inclusion or exclusion of species in comparative tests, and to use statistical methods with the same care as in the analysis of experimental results.

Tests of the quantitative predictions of optimization models in particular populations are beginning to be made. It is commonly found that a model correctly predicts qualitative features of the observations, but is contradicted in detail. In such cases, the Popperian view would be that the original model has been falsified. This is correct, but it does not follow that the model should be abandoned. In the analysis

of complex systems it is most unlikely that any simple model, taking into account only a few factors, can give quantitatively exact predictions. Given that a simple model has been falsified by observations, the choice lies between abandoning it, and modifying it, usually by adding hypotheses. There can be no simple rule by which to make this choice; it will depend on how persuasive the qualitative predictions are, and on the availability of alternative models.

Mathematical methods of optimization have been developed with engineering and economic applications in mind. Two theoretical questions arise in applying these methods in biology. First, in those cases in which the fitnesses of phenotypes are frequency-dependent, the problem must be formulated in game-theoretical terms; some difficulties then arise in deciding to what type of equilibrium a population will tend. A second and related set of questions arise when specific genetic assumptions are incorporated in the model, because it may be that a population with the optimal phenotype cannot breed true. These questions need further study, but at present there is no reason to doubt the adequacy of the concepts of optimization and of evolutionary stability for studying phenotypic evolution.

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Annual Review of Ecology and Systematics
Volume 9, 1978

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