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DEFINITION AND EVALUATION OF THE FITNESS OF BEHAVIORAL AND DEVELOPMENTAL PROGRAMS

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INTRODUCTION

> Whereas population genetics underrates the organism, life history theory underrates the gene. These fields are limited, in part because they ignore each other and in part because they ignore development. Thus the perspective of life history motivates a new look at development because developmental mechanisms could connect population genetics with life history theory to form a predictive theory of evolution more powerful than either of the first two attempted. (Bonner 1982, p. 238)

> . . . evolution can no longer be looked at solely as changes in gene frequencies within populations, or as fossil lineages: it is now essential to consider simultaneously the roles of genetics, development, ecology, and behavior (Bonner 1988, p. 24)

The definition and evaluation of fitness in terms of expected lifetime reproduction is central to our understanding of natural selection (118). In principle, fitness is defined in terms of a range of phenotypes that are the product of a single genotype; studies of such phenotypes are usually restricted to morphology. However, behavioral and developmental traits are subject to

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selection as well. Darwin used arguments concerning genetics (variation), development (embryology), ecology (geographical variation), and behavior (instinct) to support his theory. Here, we focus on dynamic programming methods to account for selection on such traits. Our intent is to explain the basic ideas of dynamic programming and to explore their applicability to the difficult problems of linking developmental, behavioral, and evolutionary phenomena. We shall show that, in principle, one can relate measurable physiological and ecological variables such as developmental times and behavioral traits to the fitness of an organism. We are far from being able to apply such methods to the calculation of the fitness of behavioral and developmental programs in most organisms, but sufficient progress has been made to warrant an exposition.

The linkage between development and evolution has consistently received attention (2, 9–11, 107). It has long been recognized (10, p. 179) that natural selection may modify developmental stages. Developmental biology typically focusses on the state of the organism and mechanisms that cause changes in this state, usually with little concern for evolutionary consequences. In contrast, in most of evolutionary biology, "fitness" is treated as an abstract concept, and the consequences of differences in fitness on gene frequencies are studied. A framework that joins these two is needed. It must perforce link states of organisms, ecological conditions, and an evolutionary measure of fitness within the constraints created by history and development.

Schmaulhausen (96) emphasized the role of development in molding the phenotype; Bonner (9) discussed (p. 165) the role of environmental cues in timing of developmental processes and considered animal behavior the pinnacle of biological complexity (10). For example, voltinism and diapause depend partially upon genetic control and partially upon environmentally controlled variables such as size and nutritional state (3, 7, 8, 14, 29, 36, 78, 100). Wilbur & Collins (117) proposed that size and growth rate together determine the initiation of amphibian metamorphosis, but they provided no means for predicting the thresholds for the onset of metamorphosis. Such a predictive theory would show how to link short-term behaviors such as foraging with life history (6, 103).

The uses of optimality go back to antiquity: when Dido founded the city of Carthage she had to enclose the greatest area she could in a bull's hide. Her solution was to cut the hide into a thin strip and form a semicircle, with part of the coast of the Mediterranean Sea as a boundary (64a, Book I, v. 519 ff). Optimality principles have been an outstanding success in physics. A prominent example is the principle of Fermat: Light rays always follow the path of shortest time connecting two points. This single principle explains curvature of light rays in a medium of varying velocity, Snell's law of refraction, the

laws of reflection, and a qualitative theory of diffraction. Classical optimality theory (generalizing the work of Fermat) was extended to the analysis of a sequence of interdependent decisions, often under the designation of "dynamic programming." These methods have been applied with great success to problems arising in industry, economics, renewable resource management (20), and behavior (68, 69). Some critics of optimality theory claim that its assumption that genotypes or phenotypes are being optimized may not be correct. We show that many advantages of optimality theories can be realized without any assumption of optimality for the genotypes or phenotypes under consideration (also see 74).

Since the time of the neo-Darwinian synthesis, fitness defined as the expected lifetime reproductive output has been favored as an organizing concept in biology (31). The abstract principle of maximization of fitness is plausible and has many fruitful outcomes, but the calculation of its consequences is full of difficulties. A significant obstacle is the necessity to relate fitness (which depends upon complete life histories, perhaps over several generations) to a multitude of localized processes at various stages. To avoid these difficulties, many of the earliest applications of optimality ideas used a surrogate for the Darwinian fitness.

One attempt to link behavior and evolution used the paradigm of maximizing the rate of intake of energy. This led to the development of *optimal foraging theory* (OFT) (47, 56, 79, 82, 83, 98, 99, 104). The theory has branched widely from the original purposes of the prediction of diet choice and patch residence. Theories based on rate maximization have not met the challenge described above due to a number of limitations.

1. The theories focus almost exclusively on optimal behavior rather than fitness. A consequence of attempts to predict "optimal" behavior is that any variation "disproves" the theory (40, 45, 79). Since, as we shall see below, a static optimum may not always contribute to an organism's fitness in the same way as a dynamic optimum, focus on the static optimum can lead to a mistaken impression of the relative importance of behavioral traits.
2. The theories assume that fitness is an increasing function of energy intake (or some other "currency") but provide no way to determine how crucial it is to achieve the optimum. Changes in the fitness corresponding to deviations from the optimum cannot be assessed.
3. The theories are concerned only with flows (of energy, matings, etc) and usually ignore the internal states of the organism.
4. In stochastic situations, the theories assume that the time period of interest is long enough that a (possibly discounted) mean rate of energy intake

solely determines behavior but is short enough that behavior is fixed and not facultative over this interval.

5. There is no easy way to deal with multiple determinants of fitness, such as those that arise in the predation-starvation trade-off. Some recent work has attempted to remedy this problem (1, 19, 97).

In summary, the difficulties of OFT and related theories are a focus on flows rather than states of organisms, the prediction of no variability at selective equilibrium, an inability to treat disparate consequences of behavior in a consistent manner, and no method for assessing evolutionary consequences of short-term behaviors. More recent theories of behavior have addressed the difficulty of assessing evolutionary consequences of short-term behaviors by means of the concept of a "common currency," a focus on states of organisms, and use of stochastic dynamic programming (49, 61, 62, 70).

Ecological applications of dynamic programming were reviewed in 1978 (111). At that time, solution techniques required large mainframe computers. Partly for this reason, such methods have been regarded as esoteric by many biologists. Rapid development of hardware and software now allows solution of relatively complex problems on microcomputers, using simple languages such as BASIC. The difficulty remains that only problems involving small numbers of state and decision variables can be handled by computers; even supercomputers can be bogged down by plausible biological problems.

Our central concept is a fitness landscape, analogous to the fitness surface developed by Sewall Wright. Instead of considering such a surface whose height (the fitness) is associated with all possible allelic combinations, we consider fitness landscapes associated with different programs of development or behavior (examples are given in Figures 1 and 2 below). The definition of the fitness landscape first involves the specification of a variety of genetic programs that control development or behavior. One must then evaluate the expected reproductive success for an ensemble of organisms which all employ the same program, but which may encounter different environments due to random influences. Dynamic iteration (62) methods make it possible to define and compute the expected reproductive success, without any assumption of optimality.

We conclude this work with some examples where ideas of dynamic programming have been used to construct optimal strategies for oviposition of parasitoids (behavioral programs), ontogenetic niche shifts and sex change (developmental programs). These strategies are more complicated than those obtained by ignoring internal states of the organism, but some of the qualitative predictions have been verified by experiments.

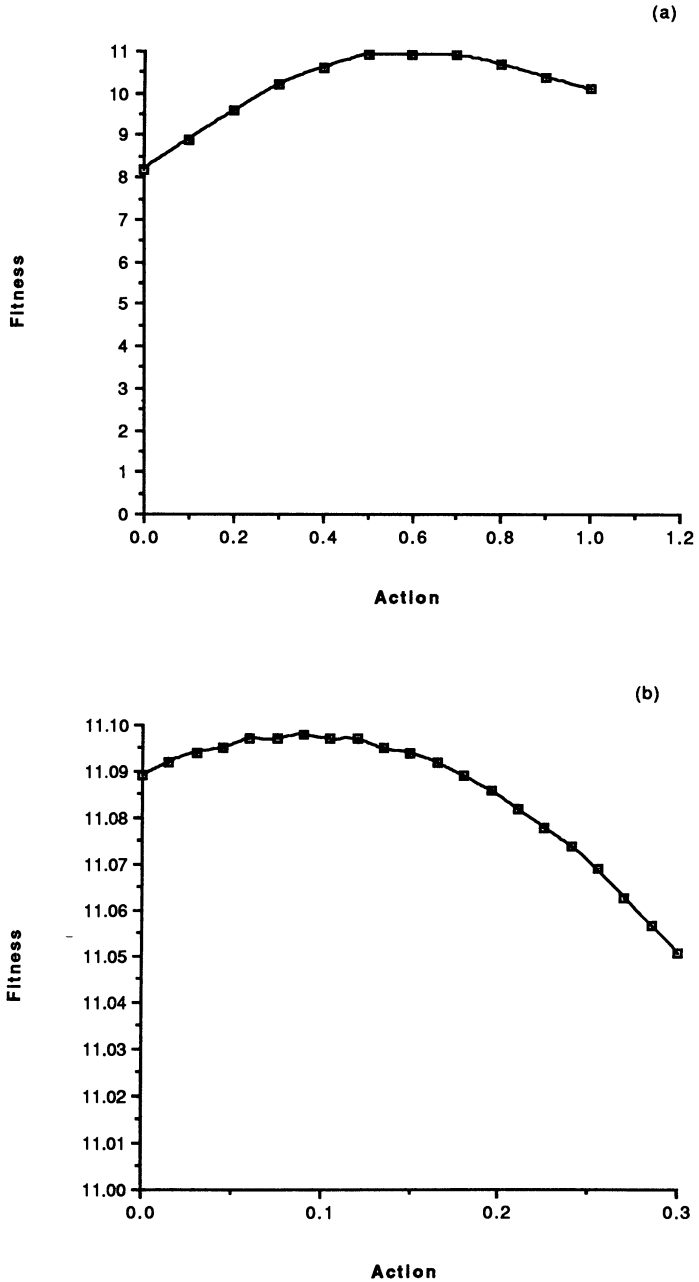
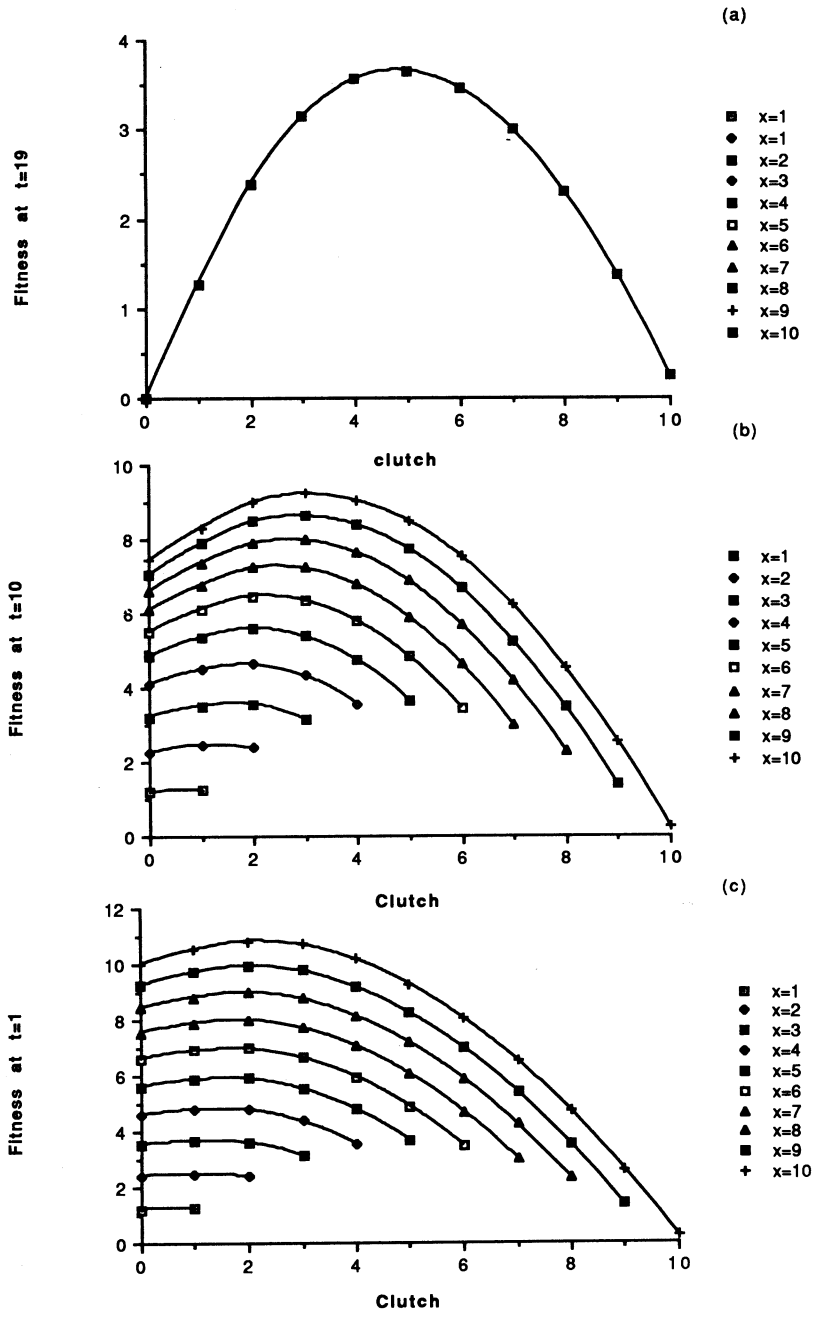


Figure 1 Fitness landscapes. (*a*) The dependence of the fourth column of Table 1 on a_1. (*b*) Fitness associated with the program Eq. 7 at $n' = 5$. Values of a_5 in the vicinity of .1 are favored, but the slight differences on the vertical axis indicate that only a slight improvement may be expected. (See discussion p. 519).


(a)
Fitness at t=19
clutch
x=1
x=1
x=2
x=3
x=4
x=5
x=6
x=7
x=8
x=9
x=10
(b)
Fitness at t=10
Clutch
x=1
x=2
x=3
x=4
x=5
x=6
x=7
x=8
x=9
x=10
(c)
Fitness at t=1
Clutch
x=1
x=2
x=3
x=4
x=5
x=6
x=7
x=8
x=9
x=10

THREE PRINCIPLES OF DYNAMIC PROGRAMMING

Our exposition is based upon three concepts:

1. The fitness function (expected lifetime reproduction) corresponding to a given program of development or behavior can be evaluated most efficiently by a "field" approach in which one constructs solutions to problems by comparing one solution with another, rather than by constructing solutions one at a time using simulation methods. Field methods were an important component of the intellectual revolution in physics (12, pg 679), and they can contribute new understanding to biological problems. Such methods require us to think in terms of families of programs or strategies instead of a single program in isolation.
2. Expected lifetime reproduction is insensitive to small deviations in programs in the vicinity of optimal programs. (In fact, this property is commonly used to determine optimal programs, as in setting the derivative of a function equal to 0 to find a maximum or minimum). The principle has the important biological implication that selection will be weak in the vicinity of optimal programs. The closer the program is to optimal, the weaker the selection (cf 47a).
3. Expected lifetime reproduction provides a "common currency" for the comparison of different programs.

None of these three concepts is new, but their generality and power are not always appreciated. We illustrate each of these concepts with a simple example, and each is developed at length in the sequel.

First Concept: The Field Approach and States of Organisms

We can illustrate the essentials of the field idea with a simple example where fitness is equated with survival, i.e. reproduction is independent of the condition of the organism (102).

EXAMPLE 1 Suppose that n represents the nutritional state of the organism, and that death results if $n = 0$, but survival is certain if n reaches a value N. Assume that during a given time interval, the probability of encountering food

←

Figure 2 The fitness landscape for insect oviposition. (*a*) Expected reproduction at $t = T-1$ corresponds to the fitness from oviposition in a single host, since there are no future opportunities. There is no dependence upon egg complement (x), except that the clutch $\leq x$. (*b*) The fitness landscape at t = 10 as a function of egg complement and clutch. Fitness is now composed of two components: reproduction in the current period plus expected future reproduction so that fitness depends upon both x and c. (*c*) The fitness landscape at $t = 1$. (See discussion p. 528)

(and increasing n by 1) is α, and the probability of not encountering food (and decreasing n by 1) is $1 - \alpha$. In this way, we have linked a physiological state with a major component (survival) of expected reproduction. We want to find the probability of guaranteed survival (i.e. the chance that the nutritional state reaches N before it reaches 0) given that the current nutritional state of the organism is n.

To answer this question, let f_n be the probability of survival, for an individual with current nutritional state n. Since death results if $n = 0$, $f_0 = 0$. When $n = 1$ there are two possibilities: either (i) food is found, or (ii) food is not found. The probability of survival if food is found is f_2. The probability of survival if food is not found is 0, since $f_0 = 0$. Since the probability of finding food is α,

$$f_1 = \alpha f_2. \qquad 1.$$

At this stage both f_1 and f_2 are unknown. What is known is that they are related by Eq. 1. In general, for an individual starting at nutritional state n

$$f_n = \alpha f_{n+1} + (1 - \alpha) f_{n-1},\ n = 1, \ldots, N-1, \qquad 2.$$

In order to express the assumptions that death is certain when n reaches 0 and survival is certain when it exceeds the value N, we add the conditions

$$f_0 = 0 \text{ and } f_N = 1. \qquad 3.$$

With the addition of conditions Eq. (3), the system Eq. (2) has the same number of equations as unknowns. Such a system can be solved without difficulty using packages available for microcomputers such as MINITAB or MATHEMATICA[1].

[1]An explicit solution can be found if we rewrite the equations in terms of the differences $g_n = f_n - f_{n-1}$. The resulting solution is:

$$f_n = (1 + R + R^2 + \ldots + R^{n-1}) \frac{1-R}{1-R^N}$$

where $R = \dfrac{1-\alpha}{\alpha}$

The approach we have taken is a standard technique in the theory of stochastic processes, whose roots are in the Hamilton-Jacobi theory of classical mechanics and optics (27). In physics, this approach has been identified with the idea of a "field," which describes the influence of distant objects upon a given object. In optics, a field describes the totality of light rays emerging from a given point. There is an analogous field concept in the more general mathematical theory of the calculus of variations. The field method eliminates action at a distance and sometimes makes it possible to solve many problems at the same time.

MacArthur & Wilson (58) used an approach similar to this one for the problem of extinction of island populations. The most important feature of such an approach is that we obtain the solutions of many problems simultaneously. In fact the method rests upon determining and solving relations between solutions rather than direct calculation of any but the simplest solutions. For example, if we were to attempt a direct solution by simulation methods, many hundreds or thousands of trials would be required to produce only limited accuracy in the answer to a single problem, with specific values of n, N, and α. The approach described here produces the solution $\{f_n\}$ of a family of problems at once; this solution is parameterized by n, N, and α.

Second Concept: Insensitivity of the Fitness Function to Changes in Programs near Optimal Programs

There is considerable debate concerning whether selection over a long enough period will lead to perfect optimization. This debate has centered on problems of matching constraints and shifting target optima. Ignoring the issue of constraints upon selection, the principle of insensitivity implies that response to selection may be expected to be slow for populations not too far from an optimal program. Thus we should not expect to observe populations following perfectly optimal programs, even in the absence of any genetic constraints.

EXAMPLE 2 In order to illustrate this phenomenon, suppose that fitness $f(a)$ depends only upon a certain behavior a, and not upon the state of the organism. Suppose further that the fitness is low at extreme choices of a, and higher for moderate choices of a. This is a behavioral analogue of stabilizing selection. In general, there might be many local maxima of f, just as there are possibly many local peaks of a Wrightian fitness surface. For the moment, let us consider a single such peak, and suppose that it is achieved at a behavior a^*, the "optimal behavior." The maximum possible fitness is $f(a^*)$, which will be termed the "optimal fitness." In the vicinity of a^*, the fitness curve is relatively horizontal. That is, the fitness of a behavior that is near a^* is close to the optimal. On the other hand, far from a^*, the fitness is substantially lower than optimal (as in Figure 1 below).

We conclude that selection will be strong on such behaviors far from a^*, but weak on nearby behaviors. For instance, if $f(a) = 1 - (a-a^*)^2$ and selection removes all but the top 1% of actions, we retain such actions as are within 10% of a^*. In order to achieve a maximum difference of 1% in actions, selection would have to remove all but the top .01% of actions. Therefore, we cannot expect that selection over a moderate time period will result in an optimal action, but only that the fitness of behaviors after selection will be close to optimal.

A related property of the fitness function near the optimal behavior is that

small deviations of behavior from the optimal have still smaller effects. This property makes optimal actions robust to a great variety of variations. For instance, if the environment varies, then actions that are optimal with respect to a given environment will have effects upon fitness that are not far from optimal, provided that the environment doesn't change too much.

Although one may not expect to find optimal behaviors in nature, a compact qualitative description of the fitness landscape is obtained by finding the local maxima and describing the behavior in the vicinity of the maxima. We then have an idea of how many peaks are present in the fitness landscape and the shape ("steepness") of those peaks. This is the sort of procedure advocated when trying to sketch a complicated curve. It is usually worthwhile to compute the local optima for use as landmarks, and to provide a standard for comparison of other behaviors or programs.

Thus optimal programs are distinctive landmarks in the landscape of all programs. Even though genetic constraints may prevent the attainment of these special programs, study of them is instructive for a number of disparate reasons.

1. A by-product of the calculation of optimal solutions is a collection of dimensionless quantities that enter into the solution. That is, a key factor in determination of an optimum may be combinations of environmental or physiological parameters. Examples are the "minimize $\frac{\mu}{g}$ rule" (115; described below) and the quantities involving marginal returns.
2. Information is used by the organism to determine an optimal solution. In nature, information is necessarily inaccurate to a certain extent. The optimality principle assures that small inaccuracies in information have a very small effect.
3. Constraints may have large effects, but not if the optimal solution nearly satisfies the constraint.
4. The fitness of the programs that contain only small deviations from the optimal program can be determined rapidly and easily.

Third Concept: Expected Lifetime Reproduction as a "Common Currency"

Frequently a behavior has both beneficial consequences such as increased food intake, and harmful consequences such as increased risk of predation. To compare such qualitatively different consequences in a consistent manner, we combine the two models described above.

EXAMPLE 3 Suppose that the chance of finding food (denoted by α) is affected by a certain behavior a; we write $\alpha = \alpha(a)$. We also assume that there is a mortality risk associated with a, which is different in character from

starvation, as in the case where foraging results in an increased hazard of predation. We denote this additional probability of mortality by $\mu(a)$. The analogue of Eq. 2 is

$$f_n = [1-\mu(a)]\ [\alpha(a)\, f_{n+1} + (1\text{-}\alpha(a))\, f_{n\text{-}1}], \qquad 4.$$

valid for $1 \leq n \leq N - 1$.

The new factor $1 - \mu(a)$ expresses the fact that survival is no longer certain. After adding the conditions of Eq. 3, we can obtain a numerical solution of Eq. 4. As yet we have not specified the behavior a. In principle a different behavior could be taken for each value of nutritional state n. As we shall see below, the most effective choices of behaviors have such a general form. They are called "feedback behaviors," since the physiological state affects behavior. The result of such calculations is a fitness vector $\{f_n, n = 1, \ldots N\}$ associated with a vector describing the program of behaviors $\{a_n, n = 1, \ldots N\}$. Although the fitness vector implicitly depends upon the behaviors and thus could be written as $f_n(\{a_n\})$, we shall not do so for notational convenience.

Envision a population that follows the behaviors $\{a_n\}$ and an invader that follows a deviant strategy at certain nutritional levels. In order to determine the effect of changes in the behaviors $\{a_n\}$ at a specified nutritional state n_1, we can examine the right-hand side of Eq. 4. One behavior may result in a greater fitness than the other, and such differences can be attributed to particular terms involving a, μ, and the fitness function f. Thus the fitness function offers a direct means of evaluating the trade-offs involved. In effect, the fitness function carries the information about the likely effects of given behavior at a given nutritional level. This is the greater benefit of the "field" approach.

PROGRAMS AND FITNESS

Programs Link Genes, Organisms and Selection

The genetic code can be interpreted as a "program" for constructing an organism from a linear sequence. This interpretation has been very successful in developmental and structural biology. We shall define a program as a collection of rules that determines the response of an organism to a set of internal and external states.

Successful programs generally utilize internally maintained states to mediate responses, instead of merely responding directly to external influences. We expect that successful organisms will have differing responses, depending upon physiological states such as hunger or fatigue. They may even respond

to a lack of information about the environment by behaving in a manner that acquires information, with no other apparent benefit.

The Fitness Landscape of Programs

The fitness landscape of programs is constructed by calculating the fitness function corresponding to a certain collection of behavioral or developmental programs. We first discuss the concept of a program in more detail and then show how optimal or locally optimal programs may be constructed. Such optimal programs are to be considered as important landmarks in the fitness landscape; we do not assume that optimality is actually realized in nature.

There are two main methods for determining the fitness associated with programs. The first is the method of simulation. Given a program, simulations provide insight into individual trajectories or the distribution of certain types of trajectories. In simulations, time is run forward, and the entire program must be specified from the outset. The fitness value of a particular program is determined by averaging over the results of simulations. Simulations emphasize the trajectory space. Evaluation of the marginal returns from incremental changes in programs (which are important in evaluating take-offs and in formulating costs and benefits in a common currency) requires rerunning the entire simulation.

The second approach is the backward or field method described in this paper. This method enables one to calculate directly the expected returns for programs and the marginal returns from incremental changes in programs. The backward approach emphasizes the program space rather than the trajectory space: to each program is associated a single family of trajectories which fills a portion of trajectory space.

EXAMPLE 4 To illustrate these ideas, we adopt a somewhat more complicated model than Eqs. 2 or 4. Suppose that the probabilities of transition from one nutritional state to another depend upon both the current state n and the behavior a_n:

$$\begin{aligned}
&\Pr[n \text{ increases to } n+1, \text{ given behavior } a] = \alpha(n,a) = a\left(1 - \frac{n}{N}\right),\\
&\Pr[n \text{ decreases to } n-1, \text{ given behavior } a] = \beta(n,a) = 1 - a,\\
&\Pr[n \text{ does not change, given behavior } a] = \gamma(n,a) = 1 - \alpha(n,a) - \beta(n,a).
\end{aligned} \tag{5.}$$

These assumptions imply that it is impossibe for n to exceed N, regardless of the action taken. In the previous case, we considered survival as a measure of fitness. We also assume that there is a reproductive payoff $R(n)$ at each time step, which is proportional to the nutritional level.

When calculating the expected lifetime reproduction, it may be that because of population growth the relative genetic contribution of future offspring is less than that for present offspring (34, p. 27 ff). This effect can be included by multiplying the expected reproduction in the next period by e^{-r}, where r is the population growth rate, so that the analogue of Eq. 4 is

$$f_n = e^{-r}\,[1 - \mu(a_n)]\,[\alpha(n,a)\,f_{n+1} + \beta(n,a)\,f_{n-1} + \gamma(n,a)\,f_n] + R(n) \quad 6.$$

The program of behavior can be represented by a vector a in which the i-th component of the vector is the behavior when the nutritional state is i. We first consider behaviors that do not depend upon n, so that the program specifies $a_n = a_1$ for all values of n (Table 1). Each row corresponds to a particular choice of a_1, and each column corresponds to a single starting value for the nutritional state n. For example, the program of behavior a = (1, 1, 1, 1, 1, 1, 1) leads to fitness vector f = (4.37, 6.29, 8.22, 10.14, 12.06, 13.99, 15.91) while the program of behavior a = (.4, .4, .4, .4, .4, .4, .4) leads to fitness vector f = (2.28, 4.91, 7.71, 10.59, 13.52, 16.47, 19.43). From examination of the table, we see that no single choice of a_1 is best for all values of n. For example, $a_1 = 1$ is best for $n = 1$ but $a_1 = .2$ is best for $n = 7$ (Figure 1a, p. 511; this figure is a simple example of a fitness landscape). In harmony with Concept 2, there is very little difference in the fitness associated with nearly optimal values of a_1. For example, at $n = 4$, fitness ranges between 10.43 and 10.93 as a_1 ranges from 0.4 to 0.9. If selection were to act upon a population that is capable only of such simple programs, selection would proceed rather slowly.

Table 1 Fitness when behavior is independent of nutritional state[1]

	Nutritional State n						
Action	1	2	3	4	5	6	7
0.00	1.00	2.80	5.24	8.19	11.55	15.24	19.19
0.10	1.23	3.26	5.86	8.90	12.24	15.82	19.57
0.20	1.52	3.78	6.51	9.57	12.83	16.24	19.74
0.30	1.87	4.34	7.15	10.15	13.27	16.46	19.69
0.40	2.28	4.91	7.71	10.59	13.52	16.47	19.43
0.50	2.71	5.43	8.14	10.85	13.57	16.28	18.99
0.60	3.15	5.85	8.41	10.93	13.44	15.94	18.44
0.70	3.56	6.15	8.53	10.86	13.19	15.51	17.83
0.80	3.90	6.31	8.51	10.68	12.85	15.02	17.18
0.90	4.17	6.35	8.40	10.43	12.47	14.50	16.54
1.00	4.37	6.29	8.22	10.14	12.06	13.99	15.91

[a]Parameters are $\mu = .3a$, $e^{-r} = .8$, $R(n) = n$, and $N = 7$.

Suppose now that a program is introduced that reacts to low levels of nutrition by increasing the value of a_1. For example, if

$$a = (1, 1, 1, .4, .4, .4, .4), \qquad 7.$$

then the fitness resulting from the numerical solution of Eq. 6 is

$$f = (4.47, 6.48, 8.62, 11.09, 13.80, 16.63, 19.52). \qquad 8.$$

This simple change in program results in fitnesses all of which are larger than the corresponding fitnesses when nutritional state is ignored, except at the highest value of n. Such a program, if it is available for selection, would be favored over the simpler one which is independent of nutritional state. This elementary model illustrates how "feedback programs," i.e. programs which take differing actions depending upon the state of the organism, may be much more effective than simpler ones.

Three parameters are required to specify a program of the type of Eq. 7, in contrast to the single parameter a. Therefore visualization of the fitness landscape is more difficult. In the present case, by varying the value 0.4 in the later components Eq. 7, we can verify that 0.4 is close to the best choice, and that small changes in this value make little difference in the fitness. Similarly we find that it is best to make the break between the third and fourth components, but the results are not sensitive to this choice. Thus the fitness landscape looks like a dome centered over the behaviors described by Eq. 7.

Allowance having been made for the possibility of feedback programs, it is natural to ask whether substantial improvement may be made by allowing all possible programs. We suppose that some organisms in the population are capable of adjusting their responses to each level of nutrition. Each possible program consists of a specification of a_n and hence seven parameters. It is rather tedious to attempt to explore such a high dimensional space. We may instead use the fitness associated with a given program as a "common currency" and ask how the program may be improved. For instance we might take the program Eq. 7 with the fitness Eq. 8. At a given value, say $n' = 5$ we may examine the behavior of the right-hand side of Eq. 6 as a function of $a_{n'}$ (Figure 1b). Clearly values of a_5 in the vicinity of .1 are favored. But the slight differences on the vertical axis indicate that only a slight improvement may be expected. In a similar way, we may guess an improvement at each of the other points leading to

$$a = (1, 1, 0.75, .48, .09, 0, 0) \qquad 9.$$

with corresponding fitness

$$f = (4.50,\ 6.53,\ 8.72,\ 11.17,\ 13.95,\ 17.16,\ 20.73), \qquad 10.$$

which represents a modest improvement over Eq. 8, even though the behaviors in Eqs. 7 and 9 differ considerably for some values of nutritional state. If this process is carried out a few more times, the results quickly settle down to

$$a = (1,\ 1,\ 0.76,\ .47,\ .16,\ 0,\ 0). \qquad 11.$$

To the accuracy shown in Eq. 10, there is no improvement in the fitness. Although the program Eq. 11 actually is optimal, there is little improvement in fitness over the simpler program Eq. 7. We conclude that selection is unlikely to produce a population following the "optimal" program Eq. 11. On the contrary, there is a large amount of freedom to vary programs, with little loss of fitness. The implication for testing behavioral theories is that it is not sufficient to compare predicted and observed behaviors. If those behaviors differ one cannot reject the optimality model without consideration of the fitness of the observed behavior (60).

Seasonal Environments

We now consider the role of time, which has been neglected up to this point.

EXAMPLE 5 Reproduction may be postponed until a final time T and a certain nutritional state n_1 may be necessary in order to reproduce. In such a case, the fitness function $f_{t,n}$ will depend upon both the nutritional state n of the organism and the time t remaining until reproduction. We define the fitness at the final time T by

$$f_{T,n} = \begin{cases} 0 \text{ if } n < n_1 \\ r(n) \text{ if } n_1 \leq n \leq N \end{cases} \qquad 12.$$

We still assume that starvation results if $n = 0$:

$$f_{t,0} = 0 \text{ for } 1 \leq t \leq T. \qquad 13.$$

When Eq. 5 is used, no assumption need be made about the fitness at $n = N$; the values $f_{t,N}$ emerge as part of the solution. Now we require relations between the fitness at earlier and later times.

The Backward Equations

Eq. 4 generalizes to a dynamic relationship

$$f_{t,n} = [1 - \mu(a)]\,[\alpha(a)\, f_{t+1,n+1} + \beta(a)\, f_{t+1,n-1} + \gamma(a)\, f_{t+1,n}],$$

$$1 \le t \le T - 1,\ 1 \le n \le N - 1. \qquad 14.$$

These equations may be solved by the following scheme ("backwards induction"): $f_{T,n}$ is given by Eq. 12. Then $f_{T-1,n}$ is obtained from Eq. 14 with $t = T - 1$. The remaining $f_{t,n}$ are obtained in succession by continuing this process for decreasing t. Note that the equations for expected reproduction are dealt with most conveniently by taking time backwards. To see why this is so, note that the Eq. 12 describes reproduction at the final time T rather than any previous time. These conditions force a solution to be computed in the backwards direction, since otherwise we would have more equations than unknowns.

This example illustrates three principles which apply to the method of backwards evaluation ("Stochastic Dynamic Programming"—SDP) of the fitness of programs:

1. *Inclusion:* With probability equal to 1, something must happen during the next interval of time.
2. *Optimality:* If one knows the optimal program from time t to T, then the optimal program is known for all $s > t$ to T as well.
3. *Sequential Coupling* (62): The fitness of a program at the end of one stage of the life cycle equals the fitness at the start of the next stage of the life cycle times the probability of surviving to the next stage. For example, the system Eqs. 13 and 14, is sufficient to determine the variables $f_{t,n}$. Each of these variables is itself the fitness associated with a particular behavioral problem. Thus the "field concept" holds in this more general case.

This example also illustrates that in general fitness will depend upon nutritional status n and the time T remaining until reproduction. Thus Eqs. 13 and 14 permit a direct calculation of the fitness, without time-consuming simulations. The key is Eq. 14, which uses relationships between the fitnesses, rather than a separate calculation ab initio for each case.

A Simple Dynamical Example

Eq. 14 is incomplete without a specification of the action $a_{t,n}$ corresponding to each time t and nutritional state n. A great variety of such actions are possible. A simple description of behavior would be to forage as intensely as possible if below a value n_1, and not to forage at all if $n > n_1$, in analogy with Eq. 7. In such a case, the action is described by

$$a_{t,n} = \begin{cases} 1 & \text{if } n \leq n_1, \\ 0 & \text{if } n > n_1. \end{cases} \qquad 15.$$

Once the program of behaviors Eq. 15 and the reproductive output $R(n)$ are given, the solution of Eq. 14 is obtained by numerical methods (62, Chapter 2). The output of such a numerical procedure is a matrix showing fitness as a function of time and nutritional state. The result if the final reproductive output $R(n) = (0, 0, 0, 0, 1, 1, 1, 1, 1, 1)$ is shown in Table 2; each row corresponds to a single time t, and each column corresponds to a single nutritional state n. The triangular array of 1's in the upper right-hand appears since $n(T) > 3$ if, for example $n(5) = 10$, and so forth. Likewise, the final state cannot exceed 3 if $n(7) = 1$. Hence the triangle of 0's in the upper left-hand corner of Table 2. Fitness always increases from left to right across rows, since the probability of starvation or a low final state decreases in the same direction. At the nutritional states $n > 3$, fitness increases as t increases but for $n = 1$ or 2, fitness first increases and then decreases with time.

The Optimal Program

It is difficult to judge the adequacy of the program Eq. 15 without a standard for comparison. The best possible program for this case is obtained in analogy with Eq. 9: at each time t and for each nutritional state n, compute $a_{t,n}$ by maximizing the right-hand side of Eq. 14. The numerical output now consists of two matrices: the first is the optimal program as a function of time and nutritional state; the second is the fitness of such optimal programs (Table 3).

The first line of the program described in Table 3 has the same consequences as the program Eq. 15, since the fitness in the lines with $t = 9$ are

Table 2 Fitness associated with the program equation (15)

	Nutritional State									
Time	1.00	2.00	3.00	4.00	5.00	6.00	7.00	8.00	9.00	10.00
10.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00
9.00	0.00	0.00	0.00	0.42	0.70	1.00	1.00	1.00	1.00	1.00
8.00	0.00	0.00	0.21	0.41	0.60	0.70	1.00	1.00	1.00	1.00
7.00	0.00	0.12	0.24	0.37	0.45	0.60	0.70	1.00	1.00	1.00
6.00	0.07	0.15	0.23	0.29	0.37	0.45	0.60	0.70	1.00	1.00
5.00	0.10	0.15	0.19	0.24	0.29	0.37	0.45	0.60	0.70	1.00
4.00	0.10	0.13	0.16	0.19	0.23	0.29	0.37	0.45	0.60	0.70
3.00	0.09	0.11	0.12	0.15	0.18	0.23	0.29	0.37	0.45	0.60
2.00	0.07	0.08	0.10	0.12	0.14	0.18	0.23	0.29	0.37	0.45
1.00	0.06	0.07	0.08	0.09	0.11	0.14	0.18	0.23	0.29	0.37

Table 3 The optimal program (*a*) and fitness (*b*) by which the simple program (15) can be evaluated

	Nutritional State									
Time	1.00	2.00	3.00	4.00	5.00	6.00	7.00	8.00	9.00	10.00
(*a*)										
9.00	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00
8.00	0.00	0.00	1.00	1.00	1.00	0.50	0.00	0.00	0.00	0.00
7.00	0.00	1.00	1.00	1.00	0.83	0.42	0.36	0.00	0.00	0.00
6.00	1.00	1.00	1.00	1.00	0.59	0.48	0.19	0.29	0.00	0.00
5.00	1.00	1.00	1.00	0.69	0.55	0.36	0.29	0.00	0.24	0.00
4.00	1.00	1.00	0.74	0.60	0.45	0.34	0.18	0.13	0.00	0.21
3.00	1.00	0.74	0.62	0.50	0.39	0.26	0.17	0.00	0.00	0.00
2.00	1.00	0.63	0.52	0.42	0.32	0.22	0.10	0.00	0.00	0.00
1.00	1.00	0.56	0.44	0.35	0.26	0.16	0.06	0.00	0.00	0.00
(*b*)										
10.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00
9.00	0.00	0.00	0.00	0.42	0.70	1.00	1.00	1.00	1.00	1.00
8.00	0.00	0.00	0.21	0.41	0.60	0.72	1.00	1.00	1.00	1.00
7.00	0.00	0.12	0.24	0.37	0.46	0.61	0.73	1.00	1.00	1.00
6.00	0.07	0.15	0.23	0.30	0.38	0.48	0.61	0.74	1.00	1.00
5.00	0.10	0.15	0.19	0.25	0.31	0.39	0.48	0.61	0.74	1.00
4.00	0.10	0.13	0.16	0.20	0.25	0.31	0.39	0.48	0.61	0.75
3.00	0.09	0.11	0.14	0.17	0.21	0.26	0.31	0.39	0.48	0.61
2.00	0.08	0.09	0.11	0.14	0.17	0.21	0.26	0.31	0.39	0.48
1.00	0.06	0.08	0.10	0.12	0.14	0.17	0.21	0.26	0.31	0.39

the same in Table 2 and the fitness array in Table 3b. For values of $t < 9$ the optimal actions differ more and more from the simple program, and the optimal fitness is accordingly higher. However, these differences need not be very large. For example at $t = 1$ we have:

Behavioral Program	Fitness for n =									
	1	2	3	4	5	6	7	8	9	10
Eq. 15	.06	.07	.08	.09	.11	.14	.18	.23	.29	.37
Optimal	.06	.08	.10	.12	.14	.17	.21	.26	.31	.39

We conclude that the simple program Eq. 15 can be improved by a program which depends upon t as well as n, but it might require considerable time for the simple program to be displaced by another. It is also clear that a great variety of programs will perform nearly as well as the optimal one. Therefore, one should not expect selection to achieve much more than a qualitative agreement between programs in nature and the optimal one.

Stationary and Nonstationary Programs

Programs like Eq. 15 that are independent of time are called "stationary," whereas those that depend upon time are called "nonstationary." Time did not appear explicitly in our example Eq. 4, and hence we considered only the possibility of stationary programs. What would happen to that example if it were made into a time-dependent problem? Suppose, for example, that we set $f_{T,n} = 0$ for all values of the nutritional variable. Including population growth in our computation of fitness, Eq. 14 becomes

$$f_{t,n} = e^{-r}[1 - \mu(a)]\,[\alpha(a)f_{t+1,n+1} + \beta(a)\,f_{t+1,n-1} + \gamma(a)\,f_{t+1,n}] + R(n),$$

$$1 \le t \le T - 1,\ 1 \le n \le N - 1. \qquad 16.$$

Once again, the numerical solution of Eq. 16 determines optimal actions and fitness associated with those actions (Table 4). We find that as t approaches 1, the actions approach the optimal stationary program Eq. 9, and the fitness also approaches the fitness that corresponds to the stationary program. The fitness corresponding to the stationary policy agrees with the fitness computed from Eq. 16, except in the second decimal digit for a few particular

Table 4 The optimal program (*a*) and fitness (*b*) when population growth is considered

	Optimal Actions Nutritional State						
Time	1.00	2.00	3.00	4.00	5.00	6.00	7.00
(*a*)							
9.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8.00	1.00	1.00	1.00	0.62	0.11	0.00	0.00
7.00	1.00	1.00	0.92	0.55	0.17	0.00	0.00
6.00	1.00	1.00	0.85	0.53	0.18	0.00	0.00
5.00	1.00	1.00	0.81	0.51	0.17	0.00	0.00
4.00	1.00	1.00	0.79	0.50	0.17	0.00	0.00
3.00	1.00	1.00	0.78	0.49	0.17	0.00	0.00
2.00	1.00	1.00	0.77	0.48	0.16	0.00	0.00
1.00	1.00	1.00	0.77	0.48	0.16	0.00	0.00
(*b*)							
10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9.00	1.00	2.00	3.00	4.00	5.00	6.00	7.00
8.00	2.04	3.52	5.00	6.53	8.20	10.00	11.80
7.00	2.85	4.56	6.29	8.17	10.24	12.56	15.00
6.00	3.42	5.25	7.14	9.22	11.55	14.19	17.05
5.00	3.79	5.69	7.69	9.90	12.40	15.24	18.35
4.00	4.04	5.99	8.05	10.34	12.94	15.92	19.19
3.00	4.20	6.18	8.28	10.63	13.30	16.36	19.73
2.00	4.30	6.30	8.43	10.82	13.53	16.64	20.08
1.00	4.37	6.38	8.53	10.94	13.68	16.82	20.31

values of time and nutritional state. We thus see that, except for values of t close to the terminal time T, behavior is either weakly dependent on time or is independent of time and that increments in lifetime fitness decrease as the time to go $T-t$ increases. Some of the strongest predictions of this theory involve changes in behavior as a time constraint is approached (57, 59, 92, 95).

The Connection with Quantitative Genetics

Recent studies of the genetic basis of behavior (80) have revealed three main features. (*a*) There is a clear genetic basis of and influence on behavior. (*b*) Heritability estimates derived from the magnitude of response to selection are nearly always less than 50%. That is, in many cases most behavioral variability is not genetic in origin. (*c*) Many genes appear to affect behavior, which suggests that methods of quantitative genetics are appropriate.

Theoretical work in quantiative genetics (4, 5, 43, 54, 55, 108) has laid the foundation for the study of the evolution of behavior and development. These theories predict how the distribution of reaction norms will change over time in response to selection. The theories, however, are not self-contained since fitness is treated as an (usually ad hoc) input. The methods developed here provide a natural way to determine the fitness function for use in the theories of quantitative genetics. One need no longer assume that lifetime fitness is normally distributed. The assumption of normality simplifies the analysis of evolution because the treatment of heredity is simplified, but sacrifices biology for this simplification. Behavioral ecology allows us to compute fitnesses associated with behavioral or developmental programs. The interaction of behavioral ecology and quantitative genetics will strengthen each.

EXAMPLES OF BEHAVIORAL AND DEVELOPMENTAL PROGRAMS AND THEIR ANALYSIS

The methods described above aid in understanding the selective forces that act upon behavior and development. The analysis usually requires some level of numerical computation to determine a solution. Such specific numerical examples aid intuition and often provide general insights.

A Behavioral Program: Clutch Size in Insect Parasitoids (41, 51, 59)

Temperate insect parasitoids (109) are ideal organisms for testing many of the ideas developed here. Because the adult parasitoids usually die at the onset of winter, the terminal time T (as in Eq. 12) is clearly defined. In many species, adults emerge with essentially a full egg complement. Thus, the physiological state variable n can be interpreted as the current egg complement. Recent

empirical work (e.g. 26, 35, 77) has shown that the number of mature eggs that a female carries clearly affects host selection.

Such parasitoids reproduce by oviposition in the larvae or pupae of other insects. The action a is the clutch of the ovipositing parasitoid. Because host volume is limited, each host can support a limited number of parasitoid larvae. In addition, the fecundity of an adult parasitoid is often directly related to its size, which in turn is directly related to resources available to it as a larvae. Thus, the per-egg fitness which an ovipositing female accumulates from oviposition in a host is usually a decreasing function of the number of eggs laid. Thus, a plot of total fitness per host (fitness per egg times the number of eggs laid) versus clutch size is "domed" (18, 59), and for a single host, there is an "optimal clutch," which maximizes the fitness obtained by the mother from oviposition in that host. The optimal clutch usually increases with host volume.

The dynamics of the state variable are

$$n_{t+1} = \begin{cases} n_t & \text{if no host is encountered, or a host is encountered but no clutch is laid, or} \\ n_t - a_t(n) & \text{if a host is encountered and a clutch of size } a_t(n) \text{ is laid.} \end{cases} \qquad 17.$$

These relations are used in Eq. 16 with appropriate modification (59, 62). The other parameters that enter into Eq. 16 are adult mortality $\mu(a)$ and the increment in fitness from oviposition in a single host. These can be determined empirically. Oviposition involves a "trade-off" between immediate reproduction (e.g. in a poorer host) and future expected reproduction (e.g. in a superior host).

The theory leads to a number of strong, qualitative predictions (59, 62). Optimal clutch sizes for a sequence of ovipositions are in general smaller than the optimal clutch size for a single host and clutches that are close to optimal produce nearly identical effects on lifetime fitness. Furthermore, increased adult survival or encounter rates with hosts will decrease optimal clutch sizes. As t approaches T, optimal clutch sizes increase. Most of these phenomena have been observed in recent experiments (92, 94).

What would we predict for the distribution of clutch sizes, in uncontrolled field observations, for which host volume varies and when parasitoids encounter hosts at different points in their lives, with different egg complements? We anticipate that any clutch smaller than the optimum clutch for a single host could be observed, with small clutches predominating (59, 62). This is exactly the case (18); the considerable variability observed in the field

is consistent with the qualitative understanding provided by the optimality model.

Visualization of the behavioral landscape (Figure 2—see p. 512) requires solution of a particular problem, with particular values of parameters. We assumed that with the time horizon $T = 20$ periods, (*a*) the ovipositing insect has at most 10 eggs, (*b*) the probability of encountering a host in a single period is 0.3, (*c*) the probability of survival from one period to the next is .99, and (*d*) the expected reproduction associated with a clutch of size c is a domed curve, as shown in Figure 2a. Even if time horizon, maximum egg load, encounter rates, and mortality rates are held constant, the behavioral landscape is a function of time, current egg load (x), and clutch laid (c). When $t = T-1$ (Figure 3a), there is no expected future reproduction, so that the fitness landscape is identical to the expected reproduction from oviposition in a

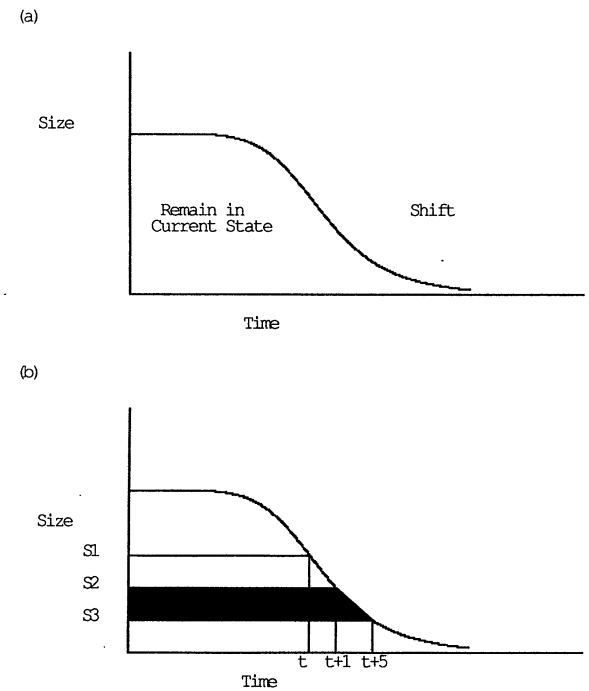


Figure 3 The state variable, dynamic theory of ontogenetic shifts or sex change leads to a "switching curve" $n_s(t)$ which describes the optimal pattern of development. For any time t before T, if the physiological variable is below the switching curve, the organism should remain in its current state whereas if the value of the physiological variable is above the switching curve, the organism should initiate a change. This theory can be tested (panel *b*) if we can find a cue which indicates that time has "jumped forward."

single host. As the time to go, $T-t$, increases, the balance between current and expected future reproduction affects the shape of the fitness landscape (Figure 2b,c). Note first the loss of fitness (expected reproduction) by laying a clutch that is smaller than optimal is generally less than the loss of fitness by laying a clutch that is larger than optimal (cf 28). This leads to the prediction that if clutches are not optimal, they are more likely to be smaller than optimal rather than larger than optimal. Second, for a fixed value of t the marginal increase in expected lifetime reproduction decreases as egg complement increases.

A Developmental Program: Ontogenetic Switching Curves (32, 33, 50, 57)

Many animals exhibit complex life cycles in which individuals undergo abrupt ontogenetic transformation (66, 113). For example, it is common that metamorphosis is associated with a shift in habitat usage. When habitats vary in risk of predation and growth rate, optimal programs often require habitat shift during ontogeny. In the first set of models of such ontogenetic habitat shifts (38, 113, 114, 115), workers concluded that the optimal behavioral program was to minimize the rate of mortality divided by the rate of growth. This is called the "minimize μ/g" strategy. This strategy can be derived from the assumption that reproduction is continuous and extends over an infinite time horizon. The predicted behavior is that all individuals will shift habitat at the same size.

Theories of sex change in sequential hermaphrodites (17) similarly assume populations with overlapping generations and a stable age distribution, corresponding to an infinite time horizon. These theories predict a single size at sex change.

Such general rules, for either habitat shift or sex change, may be broadly appropriate for interspecific comparisons. It is common, however, that reproduction is restricted to certain time periods and that the time horizon is not infinite. Considerable intraspecific variation in size dependent behaviors is common (32, 33, 105, 112, 116), and individuals often exhibit substantial variation in behavior during the course of their lives (16). In these cases, a dynamic, state variable theory of development is appropriate. Dynamic, state variable theories have been proposed for the ontogenetic niche shift (57, 95) and for sex change (33). In each case, the prediction of the theory (Figure 3a) is a "switching curve" $n_s(t)$ which indicates, at any given time, the size for an individual to initiate the developmental change.

The predictions of such an optimality theory can be tested experimentally if we can manipulate a cue which indicates that time has "jumped forward." That is, consider some intermediate time t (Figure 3b), with corresponding switching value S_1. In the following time period, the switching size will be S_2.

On the other hand, if the animals are given a cue indicating that the following period were $t+5$ instead of $t+1$, the switching value would be S_3. We thus predict that without the cue, individuals whose size was between S_3 and S_2 would not initiate developmental change, whereas those individuals who received the cue and whose size was in this interval (darkened region in Figure 3b) would initiate developmental change.

Fernandes (32) conducted such an experiment using the dusky slug *Arions subfuscus*. This slug is a protandrous hermaphrodite living in temperate climates. Essentially all individuals die at the onset of the first frost, so that T is well defined. The appropriate physiological state variable is body size, and the theory is an extension of the size-advantage hypothesis (37) to deal with time-limited life histories and intraspecific variation. Fernandes found that light cycle was a sufficient cue for developmental change, in the sense described above. As predicted by the theory (Figure 3b) when a population of slugs was subdivided randomly into a group receiving a normal light cycle (control) and a group receiving a light cycle indicating that time had shifted forward (experimental), slugs in the experimental group initiated sex change at a smaller size than slugs in the control group.

Additional Studies

In Table 5, we provide examples of a variety of other studies of behavioral and developmental programs that use dynamic, state variable approaches. This list is not intended to be comprehensive (also see Ref. 22 for additional studies).

Table 5 Other studies using dynamic state variable models[1,2]

Reference	Subject	Predictions	Exps[1]	Fitnes
13	Effect of imperfect knowledge of predation rates on fitness	A wide range of estimates of predation rate may lead to the same fitness		+
15	Physiological integration in clonal plants	Abandonment of ramets as a function of size		
21	Foraging group size in lions	Group size as a function of physiological reserves	+	
23	Diel migration by juvenile salmon	Timing of diel migration	+	
24, 25	Risks and costs of parenthood Case study of Atlantic puffins dovekie	Parental defense, provision to nestlings as function of state	+	
39	Foraging group size in lions; sensitivity analysis of dynamic models	Foraging group size as a function of physiological reserves	+	+
42	Diet selection by guppies with/without predators present	Diet composition (3 prey types)	++	

(*continue*

Table 5 (continued)

Reference	Subject	Predictions	Exps[1]	Fitness[2]
46	Timing of breeding of birds in temperature environments	Role of daylength temperature, food supply and predation in the timing of breeding	+	+
47b	Diet choice in fish	Comparison of static and dynamic models of diet choice	++	
48	Nest defense in plethodontid salamanders	When a parent should defend the nest, as a function of body size and eggs	+	+
52	Mate desertion in Cooper's hawks	Desertion as a function of physiological and ecological variables	++	+
63	Role of information in insect host choice	Superparasitism as a function of egg load and experience	+	
71	Partial preferences in foraging	Considerations associated with state variables can lead to predictions of partial preferences		
72	State-dependent contests for food	ESS behavior in the hawk-dove and war of attrition behavioral games may be state dependent and need not depend monotonically on state		
73	Daily routines of singing and foraging to attract a mate	Many, including that a peak in singing at dawn can result from variability in overnight energy expenditure even in the absence of circadian patterns	++	
76	Colony formation in social hymenoptera	Site selection for location of the colony	+	+
81	Territorial bequeathal by female red squirrels to their young	Prediction of females which will bequeath territories as a function of state and time of the season		
84	The way in which individuals acquire information about prospective mates	With search and sampling costs, sequential search for mates dominates the best-of-n strategy	+	+
90	Role of accurate information about host encounter rates in host choice	Behaviors with inaccurate information may lead to identical fitness as the case of perfect information	+	+
91	Density dependence of parasitism by fruit flies	Emergence of inverse density dependent parasitism in communities when individuals have direct density dependent parasitism	+	
93	Host (blood) and energy (nectar) seeking by mosquitoes	Seek blood under a wide variety of conditions but seek nectar only if crop volume, concentration, and energy are correct	+	
106	Behavior of small bird during the winter	Flocking as a function of energy reserves, predation risk, and mating status. Prediction of when to sing (to attract a mate) rather than flock	+	+
119	Juvenile alcid life histories	Mass of nestlings at fledging	+	

[1]A ++ indicates the experiments or field studies were conducted to test the state variable model; a + indicates comparison of the state variable model with previous empirical work.

[2]A + indicates that a fitness landscape, in addition to optimal behaviors, was computed.

CONCLUSIONS

A framework in which physiological (state) variables characterizing the organism are linked to reproductive success is required in order to account for selection on behavioral or developmental traits. Dynamic programming and related methods provide a framework for such accounting even if no assumptions about optimization are made. These methods are based on a field approach and work backwards in time, since terminal fitness can usually be assessed as a function of physiological state. The backward approach emphasizes behavioral and developmental programs rather than individual trajectories of state variables. Such methods explicitly consider the state of the organism and take development into account.

Developmental and behavioral programs are not static, but they may be stationary and thus depend only upon the physiological state of the organism. Simple rules such as rate maximization, which are common programs for the analysis of behavioral traits, may apply if there are no important internal states. Our methods allow the computation of a landscape of programs, which is a more operational version of the fitness landscape. Optimal programs, or more generally, programs whose value is insensitive to small changes, are distinctive landmarks in the landscape of all programs. Even though genetic constraints or slow selection near the optimum may prevent the attainment of these special programs, study of them is instructive.

Diversity underlies the uniqueness and fascination of biology. Dynamic, state variable methods help provide a framework in which this great diversity can be understood. Although dynamic state variable modeling as a tool in behavioral ecology was elucidated only five years ago (61, 70), these methods have been applied to a wide variety of biological situations (Table 5). We expect that empirical studies that are tests of models linking phenotypes and fitness will expand at every level (30, 89, 110) and that the description of the fitness landscape of behavior or development will become increasingly common.

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Literature Cited

1. Abrahams, M. V., Dill, L. M. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology* 70:999–1007
2. Arthur, W. 1988. *A Theory of the Evolution of Development*. New York: Wiley
3. Bargmann, C. I., Horvitz, H. R. 1991. Control of larval development by chemosensory neurons in *Caenorhabditis elegans*. *Science* 251:1243–46
4. Barton, N. H., Turelli, M. 1989. Evolutionary quantitative genetics: how little do we know. *Annu. Rev. Genet.* 23:337–70
5. Barton, N. H., Turelli, M. 1991. Natural and sexual selection on many loci. *Genetics* 127:229–55
6. Berry, R. J. 1989. Ecology: where genes and geography meet. *J. Anim. Ecol.* 58:733–59
7. Blakley, N. 1981. Life history significance of size-triggered metamorphosis in milkweed bugs (*Oncopeltus*). *Ecology* 62:57–64
8. Blakley, N., Goodner, S. R. 1978. Size-dependent timing of metamorphosis in milkweed bus (*Oncopeltus*) and its life history implications. *Biol. Bull.* 155:499–510
9. Bonner, J. T. 1974. *On Development*. Harvard Univ. Press
10. Bonner J. T. 1988. *Evolution of Complexity*. Princeton, NJ: Princeton Univ. Press
11. Bonner, J. T. 1982. *Evolution and Development*. New York: Springer-Verlag
12. Boorstin, D. J. 1985. *The Discoverers*. New York: Vintage
13. Bouskila, A., Blumstein, D. 1991. Rules of thumb for predations hazard: Predictions from a dynamic model. *Am. Nat.* 139:161–76
14. Brown, G. C., Berryman, A. A., Bogyo, T. P. 1978. Simulating codling moth population dynamics: model development, validation and sensitivity. *Environ. Entomol.* 7:219–27
15. Caraco, T., Kelly, C. K. 1991. On the adaptive value of physiological integration in clonal plants. *Ecology* 72:81–93
16. Caro, T. M., Bateson, P. 1986. Organization and ontogeny of alternative tactics. *Anim. Behav.* 34:1483–99
17. Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton, NJ: Princeton Univ. Press
18. Charnov, E. L., Skinner, S. W. 1984. Evolution of host selection and clutch size in parasitoid wasps. *Fla. Entomol.* 67:5–21
19. Chesson, P., Rosenzweig, M. L. 1991. Behavior, heterogeneity, and the dynamics of interacting species. *Ecology* 72:1187–95
20. Clark, C. W. 1976. *Mathematical Bioeconomics*. New York: Wiley
21. Clark, C. W. 1987. The lazy, adaptable lions: a Markovian model of group foraging. *Anim. Behav.* 35:361–68
22. Clark, C. W. 1991. Modeling behavioral adaptations. *Behav. Brain Sci.*14:85–117
23. Clark, C. W., Levy, D. A. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Nat.* 131:271–90
24. Clark, C. W., Ydenberg, R. C. 1990. The risks of parenthood. I. General theory and applications. *Evol. Ecol.* 4:21–34
25. Clark, C. W., Ydenberg, R. C. 1990. The risks of parenthood. II. Parent-offspring conflict. *Evol. Ecol.* 4:312–25
26. Collins, M. D., Dixon, A. F. G. 1986. The effect of egg depletion on the foraging behaviour of an aphid parasitoid. *J. Appl. Entomol.* 102:342–52
27. Courant, R., Hilbert, D. 1962. *Methods of Mathematical Physics*. Vol. II. New York: Wiley Intersci.
28. Dhondt, A. A., Andriasensen, F., Matthysen, E., Kempenaers, B. 1990. Nonadaptive clutch sizes in tits. *Nature* 348:723–25
29. Dingle, H., Mousseau, T. A., Scott, S. M. 1990. Altitudinal variation in life cycle syndromes of California populations of the grasshopper, *Melanoplus sanguinipes* (F.). *Oecologia* 84:199–206
30. Dykhuizen, D. E., Dean, A. M. 1990. Enyzme activity and fitness: evolution in solution. *Trends Ecol. Evol.* 5:257–62
31. Endler, J. A. 1986. *Natural Selection in the Wild*. Princeton, NJ: Princeton Univ. Press
32. Fernandes, D. M. 1988. *The adaptive significance of protandry in the terrestrial slug,* Arion subfuscus. PhD thesis. Dep. Biol., Princeton Univ.
33. Fernandes, D. M. 1990. Sex change in terrestial slugs: social and ecological factors. In *Sex Change and Sex Allocation: Experiments and Models,* ed. M. Mangel. Providence, RI: Am. Math. Soc.
34. Fisher, R. A. 1958. *The Genetical Theory of Natural Selection*. New York: Dover
35. Fitt, G. P. 1986. The influence of a shortage of hosts on the specifity of

oviposition behavior in species of *Dacus* (Diptera, Tephritidae) *Physiol. Entomol.* 11:133–43
36. Forrest, T. G. 1983. Insect size tactics and developmental strategies. *Oecologia* 73:178–84
37. Ghiselin, M. T. 1969. The evolution of hermaphroditism among animals. *Q. Rev. Biol.* 44:189–208
38. Gilliam, J. F. 1982. *Habitat use and competitive bottlenecks in size structured fish populations*. PhD thesis. Mich. State Univ., East Lansing, Mich.
39. Gladstein, D. S., Carlin, N. G., Austad, S. N., Bossert, W. H. 1991. The need for sensitivity analyses of dynamic optimization models. *Oikos* 60:121–27
40. Glasser, J. W. 1984. Is conventional foraging theory optimal? *Am. Nat.* 124:900–5
41. Godfray, H. C. J., Ives, A. R. 1988. Stochasticity in invertebrate clutch-size models. *Theor. Popul. Biol.* 33:79–101
42. Godin, J-G. 1990. Diet selection under the risk of predation. In *Behavioural Mechanisms of Food Selection*, ed. R. N. Hughes, pp. 739–70. New York: Springer-Verlag
43. Gomulkiewicz, R., Kirkpatrick, M. 1992. Quantitative genetics and the evolution of reaction norms. *Evolution*. In press
44. Gould, S. J. 1989. A developmental constraint in Cerion, with comments on the definition and interpretation of constraint in evolution. *Evolution* 43:516–39
45. Gould, S. J., Lewontin, R. C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. London Ser. B* 205:581–98
46. Goutis, C., Winkler, D. 1992. Hungry chicks and mortal parents: a state variable approach to the breeding season of birds. *Bull. Math. Biol.* 54:379–400
47. Gray, R. D. 1987. Faith and foraging: a critique of the paradigm argument from design. In *Foraging Behavior*, ed. A. C. Kamil, J. R. Krebs, H. R. Pulliam, pp. 69–140. New York: Plenum
47a. Hart, P. J. B. 1986. The influence of sex, patch quality, and travel time on foraging decisions by young adult *Homo sapiens* L. *Ethol. Sociobiol.* 7:71–89
47b. Hart, P. J. B., Gill, A. B. 1992. Choosing prey size: a comparison of static and dynamic foraging models for predicting prey choice by fish. In *The Behavioural Ecology of Fishes*, ed. F. A. Huntingford, P. Torricelli. London: Harwood. In press
48. Hom, C. L., Willits, N. H., Clark, C. W. 1990. Fitness consequences of nest defense in Plethodontid salamanders: predictions of a dynamic optimization model. *Herpetologica* 46:304–19
49. Houston, A. I., Clark, C. W., McNamara, J. M., Mangel, M. 1988. Dynamic models in behavioural and evolutionary ecology *Nature* 332:29–34
50. Iwasa, Y. 1991. Sex change evolution and cost of reproduction. *Behav. Ecol.* 2:56–59
51. Iwasa, Y., Suzuki, Y., Matsuda, H. 1984. Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. *Theor. Popul. Biol.* 26:205–27
52. Kelly, E. J., Kennedy, P. L. 1992. A dynamic stochastic optimization model of mate desertion in Cooper's hawks. *Ecology*. In press
53. Kirkpatrick, M. 1988. The evolution of size in size-structured populations. In *Size Structured Populations, ed. B. Ebenman, L. Persson, pp. 13–28. New York: Springer-Verlag*
54. Kirkpatrick, M., Heckman, N. 1989. A quantitative genetic model for growth, shape, reaction norms, and other infinite-dimensional characters. *J. Math. Biol.* 27:429–50
55. Kirkpatrick, M., Lofsvold, D., Bumler, M. 1990. Analysis of the inheritance, selection, and evolution of growth trajectories. *Genetics* 124:979–93
56. Krebs, J. R., Stephens, D. W., Sutherland, W. J. 1983. Perspectives in optimal foraging. In *Perspectives in Ornithology: Essays Presented for the Centennial of the Am. Ornithologists' Union*, ed. A. H. Bush, G. A. Clark Jr., pp. 165–221. Cambridge, UK: Cambridge Univ. Press. 560 pp.
57. Ludwig, D., Rowe, L. 1990. Life-history strategies for energy gain and predator under time constraints. *Am. Nat.* 135:686–707
58. MacArthur, R. A., Wilson, E. O. 1967. *Theory of Island Biogeography*. Princeton, NJ: Princeton Univ. Press
59. Mangel, M. 1987. Oviposition site selection and clutch size in insects. *J. Math. Biol.* 25:1–22
60. Mangel, M. 1991. Adaptive walks on behavioral landscapes and the evolution of optimal behavior by natural selection. *Evol. Ecol.* 5:30–39
61. Mangel, M., Clark, C. W. 1986. Towards a unified foraging theory. *Ecology* 67:1127–38
62. Mangel, M., Clark, C. W. 1988. *Dynamic Modeling in Behavioral Ecolo-*

gy. Princeton, NJ: Princeton Univ. Press
63. Mangel, M., Roitberg, B. D. 1989. Dynamic information and host acceptance by a tephritid fruit fly. *Ecol. Entomol.* 14:181–89
64. Manly, B. F. J. 1985. *The Statistics of Natural Selection*. New York: Chapman & Hall
64a. Maro, P. V. (Virgil) 19BC. *The Aeneid*. (Republished by Bantan Books, New York, 1985) 465 pp.
65. Matsuda, R. 1982. The evolutionary process in talitrid amphipods and salamanders in changing environments, with a discussion of "genetic assimilation" and some other evolutionary concepts. *Can. J. Zool.* 60:733–49
66. Matsuda, R. 1987. *Animal Evolution in Changing Environments with Special Reference to Abnormal Metamorphosis*. New York: Wiley Intersci.
67. Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge, UK: Cambridge Univ. Press
68. McFarland, D. J. 1977. Decision making in animals. *Nature* 269:15–21
69. McFarland, D. J., Houston, A. I. 1981. *Quantitative Ethology—the State Space Approach*. London: Pitman
70. McNamara, J. M., Houston, A. I. 1986. A common currency for behavioral decisions. *Am. Nat.* 127:358–63
71. McNamara, J. M., Houston, A. I. 1987. Partial preferences and foraging. *Anim. Behav.* 35:1084–99
72. McNamara, J. M., Houston, A. I. 1989. State-dependent contests for food. *J. Theor. Biol.* 137:457–79
73. McNamara, J. M., Mace, R. H., Houston, A. I. 1987. Optimal daily routines of singing and foraging in a bird singing to attract a mate. *Behav. Ecol. Sociobiol.* 29:399–405
74. Mitchell, W. A., Valone, T. J. 1990. The optimization research program: studying adaptations by their function. *Q. Rev. Biol.* 65:43–65
75. Mitchell-Olds, T., Rutledge, J. J. 1986. Quantitative genetics in natural plant populations: a review of the theory. *Am. Nat.* 127:379–402
76. Nonacs, P. 1989. Competition and kin discrimination in colony founding by social Hymenoptera. *Evol. Ecol.* 3:221–35
77. Odendaal, F. J., Rausher, M. D. 1990. Egg load influences search intensity, host selectivity, and clutch size in *Battus philenor* butterflies. *J. Insect Behav.* 3:183–93
78. Palmer, J. O. 1984. Environmental determinants of seasonal body size variation in the milkweed leaf beetle, *Labidomera clivicollis* (Kirby) (Coleoptera: Chrysomelidae). *Ann. Entomol. Soc. Am.* 77:188–92
79. Pierce, G. J., Ollason, J. G. 1987. Eight reasons why optimal foraging theory is a complete waste of time. *Oikos* 49:111–18. Also see the reply directly following the article
80. Plomin, R. 1990. The role of inheritance in behavior. *Science* 248:183–88
81. Price, K. 1992. Territorial bequeathal by red squirrel mothers: a dynamic model. *Bull. Math. Biol.* 54:335–54
82. Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* 15:523–75
83. Pyke, G. H., Pulliam, H. R., Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52:137–54
84. Real, L. 1990. Search theory and mate choice: I. Models of single-sex discrimination. *Am. Nat.* 136:376–404
85. Real, L., Caraco, T. 1987. Risk and foraging in stochastic environments. *Annu. Rev. Ecol. Syst.* 17:371–90
86. Riechert, S. E., Hammerstein, P. 1983. Game theory in the ecological context. *Annu. Rev. Ecol. Syst.* 14:377–409
87. Riska, B. 1986. Some models for development, growth, and morphometric correlation. *Evolution* 40:1303–11
88. Roe, A., Simpson, G. G. 1958. *Behavior and Evolution*. New Haven, Conn: Yale Univ. Press
89. Roff, D. 1980. On defining sufficient causes for natural selection to occur. *Evol. Theory* 4:195–201
90. Roitberg, B. D. 1990. Optimistic and pessimistic fruit flies: evaluating fitness consequences of estimation errors. *Behaviour* 114:65–82
91. Roitberg, B. D., Friend, W. G. 1992. A general theory for host seeking decisions in mosquitoes. *Bull. Math. Biol.* 54:401–12
92. Roitberg, B. D., Mangel, M., Lalonde, R., Roitberg, C. A., van Alphen, J. J. M., Vet, L. 1991. Dynamic host shifts by a parasitoid. *Behav. Ecol.* 3:156–65
93. Roitberg, B. D., Mangel, M., Tourigny, G. 1990. The density dependence of parasitism by tephritid fruit flies. *Ecology* 71:1871–85
94. Rosenheim, J. A., Rosen, D., Rossler, Y. 1990. Foraging and oviposition decisions in the parasitoid *Aphytis lingnanesis:* distinguishing the influence of egg load and experience. *J. Anim. Ecol.* 60:873–94
95. Rowe, L., Ludwig, D. 1991. Size and timing of metamorphosis in complex life

cycles: time constraints and variation. *Ecology* 72:413–27
96. Schmaulhausen, I. I. (1949). 1986. *Factors of Evolution. The Theory of Stabilizing Selection.*
97. Schmitz, O. J., Ritchie, M. E. 1991. Optimal diet selection with variable nutrient intake: balancing reproduction with risk of starvation. *Theor. Popul. Biol.* 39:100–14
98. Schoener, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369–404
99. Schoener, T. W. 1987. A brief history of optimal foraging ecology. In *Foraging Behavior,* ed. A. C. Kamil, J. R. Krebs, H. R. Pulliam, pp. 5–68. New York: Plenum
100. Scott, S. M., Dingle, H. 1990. Developmental programmes and adaptive syndromes in insect life-cycles. In *Insect Life Cycles,* ed. F. Gilbert, pp. 69–85. New York: Springer-Verlag
101. Slatkin, M. 1987. Quantitative genetics of heterochrony. *Evolution* 41:799–811
102. Slobodkin, L. 1964. The strategy of evolution. *Am. Sci.* 52:342–57
103. Southwood, T. R. E. 1988. Tactics, strategies and templets. *Oikos* 52:3–18
104. Stephens, D. W., Krebs, J. R. 1986. *Foraging Theory*. Princeton, NJ: Princeton Univ. Press
105. Sweeney, B. W., Vannote, R. L. 1978. Size variation and the distribution of hemimetabolous insects: two thermal equilibrium hypotheses. *Science* 200:444–46
106. Szekely, T., Sozou, P. D., Houston, A. I. 1991. Flocking behaviour of passerines: a dynamic model for the nonreproductive season. *Behav. Ecol. Sociobiol.* 28:203–13
107. Thomson, K. S. 1988. *Morphogenesis and Evolution*. New York/Oxford: Oxford Univ. Press
108. Turelli, M., Burton, N. H. 1990. Dynamics of polygenic characters under selection. *Theor. Popul. Biol.* 38:1–57
109. Waage, J., Greathead, D. 1986. *Insect Parasitoids*. New York: Academic
110. Wade, M. J., Kalisz, S. 1990. The causes of natural selection. *Evolution* 44:1947–55
111. Walters, C. J., Hilborn, R. 1978. Ecological optimization and adaptive management. *Annu. Rev. Ecol. Syst.* 9:157–88
112. Warner, R. R. 1988. Sex change in fishes: hypotheses, evidence and objections. *Environ. Biol. Fishes* 22:81–90
113. Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk and the optimal size at transformation. *Am. Nat.* 128:319–41
114. Werner, E. E. 1988. Size, scaling and the evolution of complex life cycles. In *Size-Structured Popululations,* ed. B. Ebenman, L. Persson. New York: Springer-Verlag .
115. Werner, E. E., Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size structured populations. *Annu. Rev. Ecol. Syst.* 15:393–425
116. Wilbur, H. M. 1980. Complex life cycles. *Annu. Rev. Ecol. Syst.* 11:67–93
117. Wilbur, H. M., Collins, J. P. 1973. Ecological aspects of amphibian metamorphosis. *Science* 182:1305–14
118. Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton Univ. Press
119. Ydenberg, R. C. 1989. Growth-mortality trade-offs and the evolution of juvenile life histories in the alcidae. *Ecology* 70:1494–506