

Modeling behavioral adaptations

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Abstract: Optimization models have often been useful in attempting to understand the adaptive significance of behavioral traits. Originally such models were applied to isolated aspects of behavior, such as foraging, mating, or parental behavior. In reality, organisms live in complex, ever-changing environments, and are simultaneously concerned with many behavioral choices and their consequences. This target article describes a dynamic modeling technique that can be used to analyze behavior in a unified way. The technique has been widely used in behavioral studies of insects, fish, birds, mammals, and other organisms. The models use biologically meaningful parameters and variables, and lead to testable predictions. Limitations arise because nature's complexity always exceeds our modeling capacity.

Keywords: adaptation; behavioral ecology; control theory; dynamic programming; economic models; evolution; fitness; game theory; optimization

1. Introduction

Behavioral ecology, a branch of evolutionary biology, is concerned with understanding behavior in terms of natural selection. In searching for the ultimate causes of observed behavioral traits, behavioral ecologists frequently use optimization models (Krebs & Davies 1984). An early example was David Lack's (1954) model of optimal clutch size. Manipulation experiments had shown that most birds are capable of raising larger clutches than they do. Lack hypothesized that, rather than maximizing clutch size, natural selection would tend to maximize the average number of surviving offspring. In mathematical terms this amounts to maximizing the expression $np(n)$, where n denotes clutch size and $p(n)$ is the probability that an individual egg in a clutch of n eggs will survive to independence. Since $p(n)$ is likely to be a decreasing function of n , this hypothesis implies a smaller clutch size than the maximum possible.

Lack's model has been extensively tested; it still appears to predict larger clutches than are usually observed in nature (Klomp 1970). Ornithologists continue to study the reasons this may be so (e.g., Boyce & Perrins 1987).

Lack's is an excellent example of what I like to call a "first generation" model: simple, and readily testable. More often than not such models ultimately fail, but this certainly does not mean that they are worthless. They may still help us organize our thoughts more rigorously and ask more incisive questions. They may then be replaced by second-generation models, typically more complex, which are then tested and perhaps further modified, or replaced.

Biology is quite different from the physical sciences in the way that it uses models (Mayr 1982). Because of the great complexity present at every level in biological systems, the final "correct" model virtually never exists. Further refinements are always possible, and additional

detail can always be taken into consideration. Some biologists therefore seem to believe that mathematical models are a complete waste of time (e.g., Pierce & Ollason 1987), whereas others see them as essential (Maynard Smith 1978). As a modeler, my own view is that models can be tremendously helpful, provided that modeling is treated as a process of successive approximation to the complexity of nature.

Most of the first-generation models in behavioral ecology treated single decisions, or sequences of similar decisions – defending a territory, selecting a prey patch or item, providing parental care, and so on. Behavior is an essentially dynamic process, however: An individual's lifetime reproductive success is determined by its behavior over an extended time span. Past behavior affects an animal's current state; present behavior is influenced by this state, and affects future states and hence future behavior. Many models either ignored these dynamic implications, or finessed them by some form of time-averaging. For example, in foraging theory it was often the custom to use the average net rate of energy gain as a fitness "currency," on the assumption that while foraging, animals should be expected to maximize this average. One obvious criticism of this assumption is that variance in feeding rates might also be important. Experimental evidence appears to indicate that foragers are indeed often risk-sensitive, in the sense that both means and variances are taken into consideration (Caraco 1983; Real & Caraco 1986). Temporal variation in food intake is important because of the existence of constraints on a forager's state: Stomach capacity is limited, and most animals cannot store and preserve large quantities of food.

State variables (both internal and external) and their dynamics probably influence every behavioral act to some extent. In the case of clutch-size, raising a large clutch may have an effect on the parent's state, resulting

in decreased probability of survival. A dynamic model of parental behavior could thus be developed; the qualitative predictions of such a model can easily be foretold; quantitative testing might be formidable, but certainly not impossible.

The purpose of this target article is to outline a unified approach to the modeling and testing of dynamic state-variable models of behavior. This approach has recently been developed and applied to behavioral phenomena, by Houston & McNamara (1988a), Mangel & Clark (1988), and others. The present article is in part a follow-up to the previous BBS target article of Houston & McNamara (1988a). I hope to show that the framework described by Houston & McNamara has broader applicability than may have been apparent to some readers. I also hope that appreciation of the breadth and flexibility of dynamic modeling will dispel many of the misgivings expressed by Houston & McNamara's peer commentators.

2. The behavioral landscape

Figure 1 is a schematic representation of the relationships between an individual organism's current environment and its behavioral response to that environment. For simplicity, the time dimension is discretized into periods of convenient unit length. At the beginning of a particular period, t , the individual has an internal physiological state $X(t)$, in general a highly multidimensional entity. The individual is situated in an environment characterized by the current environmental state $Y(t)$, likewise multidimensional. Upon observing the environmental state, the organism "decides" upon a behavioral act $A(t)$, which affects its own state and possibly also the environmental state. The act $A(t)$ may also result in immediate reproductive output $R(t)$. As a result of this act, as well as of other effects beyond the control of the individual, the

state variables change to new values $X(t + 1)$, $Y(t + 1)$ in the next time period; these changes frequently involve stochastic elements. The process is continued in subsequent time periods $t + 1$, $t + 2$,

Although it is in many respects a caricature of any real behavioral landscape, Figure 1 illustrates the dynamic complexity of the world in which all organisms live and reproduce. Each of the state variables $X(t)$ and $Y(t)$ is itself immensely complex: The individual's state $X(t)$ involves morphological, physiological, psychological, and neural components (including the organism's current assessment of its environment); the environmental state $Y(t)$ includes the physical environment, as well as the biological environment, the latter consisting of food resources, competitors, predators, parasites, potential mates, and kin. All these components interact dynamically in complex ways that may influence and be influenced by the individual's behavior.

No comprehensible model can hope to encompass more than a small part of this vast complexity. Reductionism is essential for scientific progress. Restrictions and simplifications are always made by the various disciplines that study the behavioral landscape. Mathematical models are a natural, if not inescapable way to formulate and test evolutionary hypotheses. One builds a behavioral model, uses mathematical techniques to compute the "optimal" behavior according to the model, and tests the predictions against field or laboratory data.

3. Dynamic state-variable models

An animal's current state may affect its behavior in many ways. A hungry forager may accept food items that it would reject when well fed; it may also tend to be less vigilant towards predators. Animals that have territories normally do not behave towards conspecifics in the same way as those lacking territories, and so on. Conversely, behavior usually affects states; often the direct purpose of a behavioral act is to improve the individual's state in some way. Behavior is therefore affected by past events (which influence present states) and by the anticipation of future events. Past, present, and anticipated future environmental states likewise influence behavioral decisions. This is part of the behavioral landscape. Dynamic state-variable models provide a way to analyze all of these influences and relate them to reproductive fitness.

Any such model must still abstract and simplify considerably. It must first be decided which state variables are sufficiently important to be included in the model (Mangel & Clark 1988, Ch. 8). Let $X(t)$ and $Y(t)$ denote these model state variables. Next the modeler specifies the set of behavioral acts $A(t)$ to be considered. This is typically determined by the observations in need of an evolutionary explanation: How does the observed behavior contribute more to fitness than available alternatives do? An example described in the next section illustrates these and other modeling decisions.

Dynamic changes in the state variables must also be specified. For the individual's state, these changes depend on the current states $X(t)$ and $Y(t)$, and on the current act $A(t)$, and perhaps also on certain random variables denoted by $w(t)$:

$$X(t + 1) = G(X(t), Y(t), A(t), w(t)). \quad (1)$$

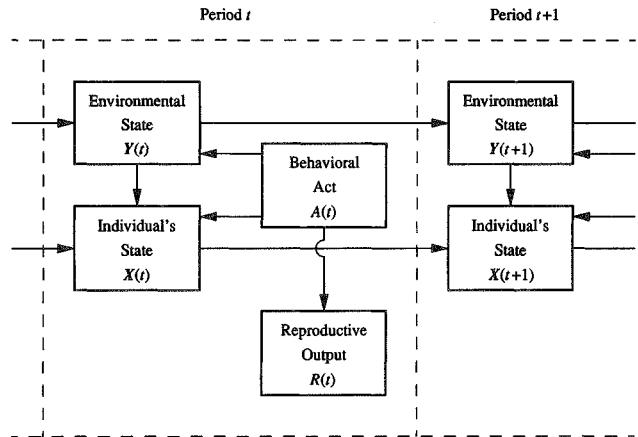


Figure 1. The behavioral landscape: The individual's state $X(t)$ in period t is influenced by the current environmental state $Y(t)$ and by the behavioral action $A(t)$ taken by the individual. The states $X(t)$ and $Y(t)$ change to new states $X(t + 1)$ and $Y(t + 1)$ in the next period $t + 1$; these changes may involve stochastic elements, i.e., they may be Markov processes. The behavioral act $A(t)$ may also affect the environmental state, and may result in reproductive output $R(t)$. The process is repeated in subsequent periods $t + 1$, $t + 2$,

The probability distributions of the random variables $w(t)$ must also be specified. (In mathematical terminology, Equation (1) defines $X(t)$ as a "Markov decision process;" see e.g. Heyman & Sobel 1984; familiarity with this topic is not assumed in what follows.) In practice, the state dynamics will usually be specified in a fairly simple form (see sect. 5); field or laboratory data may be used to estimate the parameters in this equation (sect. 7).

For the sake of simplicity I will ignore the environmental state variable $Y(t)$ in the rest of this discussion. Some of the complications that may arise when $Y(t)$ is explicitly modeled are discussed in section 8.

The modeler must finally specify the effect of behavioral decisions on fitness. If explicit reproductive activity is under consideration, the model can equate fitness with total reproduction. In many cases, however, one may be interested in behavior that is not immediately associated with reproduction. Nevertheless, ultimate reproductive success must somehow be taken into account if a model is to have any explicit evolutionary content.

To make this more precise, suppose we wish to model behavior over a time interval not involving actual reproduction. Let $t = 1, 2, \dots, T$ represent the time periods of interest. At the terminal time T the individual's state is $X(T)$. Future reproduction will inevitably depend on this terminal state (terminal from the model's standpoint, not the individual's). For example, if the individual fails to survive to T , then future reproduction is clearly zero. More generally, individuals that are in "good condition" at time T will generally have increased subsequent reproductive success. In mathematical notation,

$$\text{Expected future reproduction (at time } T\text{)} = \Phi(X(T)) \quad (2)$$

where Φ is some function relating future reproduction to the individual's state at time T . Specifying this relationship is part of the modeling process, requiring the same sort of simplifying compromises and parameter estimations as in the rest of the process (see section 7).

Having completed the construction of the model, the modeler must next figure out the optimal behavioral strategy, $(A(t))$ that results in maximum expected total lifetime reproductive success. This may seem a formidable task, even in the simplified model version of the behavioral landscape. Indeed, without the aid of today's computers, the problem simply could not be solved in most cases. The next section describes a computer-oriented algorithm that can be used to solve such problems.

4. Dynamic programming

Dynamic programming is a method of solving dynamic optimization problems, popularized by Richard Bellman (1957) at the time when digital computers were first becoming available to the scientific community. Its conceptual basis is extremely simple: We wish to determine the optimal behavior $A(t)$ for each time period $t = 1, 2, \dots, T$. We also wish to allow $A(t)$ to depend upon the individual's current state $x = X(t)$ (and in general also on the environmental state $Y(t)$, but I am suppressing this dependence now, for simplicity).

Dynamic programming proceeds one step at a time, starting with the terminal period T . According to the

assumption of Equation (2), no behavioral decision is involved in period T itself, since total expected future reproduction is specified in terms of $X(T)$, the individual's state at the beginning of period T . (This is simply a notational convenience, facilitating exposition.)

Consider the penultimate time period $t = T - 1$. A single behavioral decision is to be made during this period. If the act $A(t) = a$ is chosen, we then have, according to Equation (1)

$$X(T) = G(x, a, w), \quad x = X(T - 1), \quad w = w(T - 1), \quad (3)$$

i.e., $X(T)$ is determined by the current period's state, $X(T - 1)$ and the action taken, a ; it is also affected by the random variable $w(T - 1)$. Fitness from T on is therefore, by Equation (2)

$$\Phi(X(T)) = \Phi(G(x, a, w)). \quad (4)$$

Assuming that no reproduction occurs during period $T - 1$, we conclude that the optimal action a is that which maximizes the function on the right of Equation (4). More precisely, since this is still a random function, a must maximize the expectation (i.e., average) of this random function:

$$a \text{ maximizes } E_w\{\Phi(G(x, a, w))\}. \quad (5)$$

where E_w denotes the usual mathematical expectation (average) with respect to the random variable w . To repeat, the optimal behavior in period $T - 1$ maximizes the individual's expected future reproduction, as influenced by that decision and as expressed by Equation (5). The optimal behavioral decision in general depends upon the current physiological state $x = X(T - 1)$ of the individual. (The case of additional reproduction during period $T - 1$ is discussed in section 6.)

If a^* denotes this optimal behavioral act, we have shown that the expression

$$E_w\{\Phi(G(X(T - 1), a^*, w))\} \quad (6)$$

represents the individual's expected future lifetime reproduction, measured at the beginning of period $T - 1$. In analogy with Equation (2) we now denote this by

$$\Phi_{T-1}(X(T - 1)) \quad (7)$$

where the subscript $T - 1$ implies that the "future" now includes period $T - 1$. Thus $\Phi_{T-1}(X(T - 1))$ plays exactly the same role at time $T - 1$ as the function $\Phi(X(T))$ at time T .

We have now achieved a position of the type preferred by the mathematician: We have reduced the original optimization problem over T steps ($1, 2, \dots, T$) to an exactly equivalent problem over $T - 1$ steps ($1, 2, \dots, T - 1$). The same procedure can therefore be applied to this problem, and then repeated step by step, going from $T - 1$ to $T - 2$, then from $T - 2$ to $T - 3$, and so on. This is the dynamic programming algorithm.

Writing the algorithm out explicitly, we have from Equations (5)–(7)

$$\Phi_{T-1}(X(T - 1)) = \underset{a}{\text{maximum}} \quad E_w\{\Phi_T(G(X(T - 1), a, w)\}) \quad (8)$$

where we have written $\Phi = \Phi_T$ to emphasize that Φ refers to the final time period T . Eq. (8) also holds for $T - 1$ replaced by $T - 2$, and then for $T - 2$ replaced by $T - 3$, and so on. In general we therefore have

$$\Phi_t(x) = \underset{a}{\text{maximum}} E_w\{\Phi_{t+1}(G(x,a,w))\}, x = X(t), \quad (9)$$

for $t = 1, 2, \dots, T - 1$.

This is referred to as Bellman's dynamic programming equation. The function $\Phi_t(x)$ is called the "value function" in the dynamic programming literature, but in the present setting the term "lifetime fitness function" seems more appropriate (see Mangel & Clark, 1988, who use the notation $F(x,t,T)$ in place of $\Phi_t(x)$).

The computer implementation of Equation (9) follows the same course as the argument used to derive it, namely, one begins with $t = T - 1$, in which case the expression on the right side of Equation (9) is completely specified; the maximum is found by the computer. One thus obtains both the values of $\Phi_{T-1}(x)$ for all x , and the optimal behavioral strategy $a = a^*(x, T - 1)$ for period $T - 1$, also depending on $x = X(T - 1)$. The computation is then repeated for $t = T - 2$, and so on. A single program subroutine is used iteratively to find $a^*(x,t)$ and $\Phi_t(x)$. (The procedure is described further by Houston & McNamara 1988a, and Mangel & Clark 1988; the latter go into the details of computer programming.)

5. Applications

To illustrate dynamic modeling in a practical setting, I will now briefly describe a model due to Ydenberg (1989), concerning the fledging behavior of common murre (*Uria aalge*) chicks. Its purpose is to interpret observed fledging behavior, i.e., the murre's age and weight at fledging, in adaptational terms. This problem clearly calls for dynamic modeling.

Let t denote the age of the murre chick, measured in days from hatching, and let $W(t)$ denote its weight in grams at the beginning of day t . Also let $H(t)$ denote the chick's location at the beginning of day t , with $H(t) = 0$ if it is still in the nest and $H(t) = 1$ if it has fledged. The model's state variable $X(t)$ then has the two components $W(t)$ and $H(t)$.

While in the nest the chick grows at the daily rate $g_0(x)$; after fledging the growth rate is $g_1(x)$. These growth functions are estimated from published data on common murre weight profiles; for obvious reasons, the data on nestling weight are more complete than those for birds at sea. The explicit functions as estimated by Ydenberg were

$$\begin{aligned} g_0(x) &= 0.2x(1 - x/220) \text{ g/d,} \\ g_1(x) &= 30(1 - (x/1000)^2) \text{ g/d.} \end{aligned}$$

Thus growth at sea exceeds growth in the nest, at all weight levels.

Next, let μ_0 and μ_1 denote daily mortality risk for nestling and fledgling, respectively. The estimated values are

$$\mu_0 = 0.005 \text{ per day, } \mu_1 = 0.01 \text{ per day.}$$

A tradeoff therefore exists between safety in the nest and increased growth at sea. Since growth in the nest decreases to zero over time, the balance eventually shifts towards leaving the nest. This dynamic tradeoff between growth and survival is the explanatory device assumed in Ydenberg's model. A further possible tradeoff exists, if the risk of being killed in the act of fledging depends on fledging weight. Ydenberg does not treat this possibility,

simply assuming a fixed probability $p_f = 80\%$ of surviving the act of fledging.

To complete the model, let T denote the end of the breeding season; the chick must fledge by age T . The value $T = 90$ d is used in the model. Let $S(W(T))$ represent the probability that the fledged chick of weight $W(T)$ survives from time T to reach adulthood. On the basis that fledged murre chicks of weight less than 700 g are seldom observed, Ydenberg postulates the functional form

$$S(w) = k(w - 700)$$

where k is a positive constant (the value of which has no influence on the model's predictions). This is clearly an ad hoc choice for $S(w)$, forced by the lack of data pertaining to the relationship between juvenile weight and ultimate survival and breeding success for murres.

The dynamic programming equation for Ydenberg's model can now be derived. Let $\Phi_t(w,h)$ denote lifetime fitness (cf. Equation 9) at the beginning of day t , with $W(t) = w$, $H(t) = h$. For the final period T we have

$$\begin{aligned} \Phi_T(w,1) &= S(w) \\ \Phi_T(w,0) &= p_f S(w) \end{aligned}$$

i.e., if already fledged ($h = 1$) the chick of weight w survives to adulthood with probability $S(w)$; if not fledged, the chick must fledge (probability of survival p_f), after which it faces the same situation as before.

For $t < T$ we obtain:

$$\begin{aligned} \Phi_t(w,1) &= (1 - \mu_1)\Phi_{t+1}(w + g_1(w), 1) \\ \Phi_t(w,0) &= \underset{a}{\text{maximum}} [(1 - \mu_0)\Phi_{t+1}(w + g_0(w), 0), \\ &\quad p_f(1 - \mu_1)\Phi_{t+1}(w + g_1(w), 1)] \end{aligned}$$

These equations are easily derived as follows. If the chick has already fledged at time t ($H(t) = 1$), then it survives to time $t + 1$ with probability $1 - \mu_1$, and grows by the amount $g_1(w)$, so that its fitness at time $t + 1$ equals $\Phi_{t+1}(w + g_1(w), 1)$ with probability $1 - \mu_1$ (and zero with probability μ_1). To derive the second equation, we consider the outcomes of the two decision alternatives on day t , remain in the nest or fledge. The first term in square brackets equals the chick's fitness if it remains in the nest, and the second corresponds to fledging. The optimal strategy is the one that gives the greater fitness. These two equations constitute the dynamic programming algorithm for Ydenberg's model.

The dynamic programming equations can now be solved to determine the optimal fledging strategy; the results are shown in Table 1. These predictions agree

Table 1. Optimal age and weight of fledging for murres.

| Age, t (days) | Fledge if and only if weight exceeds |
|-----------------|--------------------------------------|
| 5 | 205g |
| 10 | 200g |
| 15 | 195g |
| 20 | 190g |
| 25 | 150g |
| 30 | 0g |

[Source: from Ydenberg 1989, Figure 5.]

Table 2. Some recently published dynamic programming models.

| Reference | Species | Behavior | Main Prediction | Empirical (E) or Theoretical (T) |
|-------------------------|--|---------------------------|---|--|
| Mangel 1987 | Parasitic wasps (<i>Nasonia vitripennis</i>) | Oviposition | Stochastic facultative variation in clutch size | E |
| Clark 1987 | Lions (<i>Panther leo</i>) | Hunting | Relations between group size and prey type | E |
| Houston & McNamara 1987 | Birds | Singing | Dawn and dusk chorus | T |
| Clark & Levy 1988 | Sockeye salmon (<i>Oncorhynchus nerka</i>) | Vertical migration | Timing of daily migrations | E |
| Ydenberg & Clark 1989 | Western grebes (<i>Aechmophorus occidentalis</i>) | Diving | Patterns of aerobic and anaerobic diving | E |
| Clark & Ydenberg 1990 | Dovekies (<i>Alle alle</i>) | Parent-offspring conflict | Weight recession prior to fledging | E |
| Lucas & Walter 1988 | Carolina chickadees (<i>Parus carolinensis</i>) | Food caching | Environmental influences on caching behavior | E,T |

reasonably well with the published data (fledging age from 18–25 days, weight from 150–220 gm). The model also suggests a negative correlation between age and weight at fledging, a prediction that is well supported by the data. Ydenberg concludes that the model is successful and “provides a good general framework for understanding the selective forces [affecting] fledging age and weight . . .” The purpose of discussing this model here, however, has simply been to indicate the practical applicability of dynamic behavioral modeling.

Table 2 lists several additional dynamic-programming models of behavior. The reader may note the wide range of species and behaviors encompassed by this list. In most cases the observed behavior could not have been analyzed successfully without using a dynamic model; in other cases the dynamic model provides insights and predictions that differ from earlier studies. All of these models, however, are what I refer to in section 7 as “first-generation” models.

6. Some misconceptions

The peer commentaries on Houston & McNamara (1988a) expressed a number of misgivings about the dynamic programming approach to behavioral modeling. Table 3 lists eight of these misgivings, each of which I feel is the result of misconceptions. I shall discuss these misconceptions in turn.

Terminal reward function. Houston & McNamara identified the specification of the terminal fitness function $\Phi(X(T))$ as a major difficulty of the dynamic programming approach. For several reasons I believe the problem to be much less severe than they suggest. First, $\Phi(X(T))$ has biological meaning, since it represents expected future reproductive success, i.e., reproductive value (Fisher 1930). (Houston & McNamara’s term “reward function” fails to emphasize this important point.) The general form of this function is often intuitively clear – it is usually nondecreasing in the state variable x (within limits – e.g.,

Table 3. Some misconceptions about dynamic programming models of behavior.

| Assertion | Commentators* |
|---|--|
| 1. Terminal reward function is hard to specify, but strongly influences predictions. | Barnard, Caraco, Huntingford & Metcalfe, Reid, Sherry, Sih, Stenseth, Timberlake |
| 2. Dynamic programming models are too general, capable of predicting almost anything, and untestable. | Huntingford & Metcalfe, King & Logue, Partridge, Reid, Timberlake |
| 3. Reproduction is not included, so that the models have no direct connection with Darwinian fitness. | Calder, Huntingford & Metcalfe, Morse, Stenseth |
| 4. Evolution does not necessarily lead to optimal behavior; there is experimental evidence of non-optimal behavior (e.g. the matching law). | Heyman, Fantino |
| 5. Terminal time may be hard to specify, but strongly influences predictions | Huntingford & Metcalfe, Rachlin, Timberlake |
| 6. Dynamic programming models are overly complex; animals use simple decision rules | Heiner, Yoerg |
| 7. Testing the model’s predictions requires measurement of state variables. | Smith, Yoerg |
| 8. Solving a dynamic model backwards in time is artificial, and ignores the organism’s past. | Barnard, Morse |

*All references are Behavioral and Brain Sciences 11 (1988), and occurred as peer commentaries to Houston & McNamara (1988a).

an overweight bird might experience difficulty flying, or be more subject to capture by a predator), and often involves a threshold value of x , below which survival or reproduction become unlikely. When a precise characterization is necessary, the determination of $\Phi(X(T))$ by actual measurement of the relationship between state variables and future reproduction is certainly not unthinkable (see section 7).

Dynamic programming models exhibit an important convergence property, in the sense that the optimal strategy $A^*(x,t)$ converges to a stationary strategy $A^*(x)$ that is independent of t , as the "time to go" $T - t$ increases (Mangel & Clark 1988, p. 232; McNamara 1990; McNamara & Houston 1982). Moreover, $A^*(x)$ is independent of the terminal fitness function. Consequently, if one is interested in modeling behavior not associated with the anticipation of future changes in external conditions beyond the horizon T , then a precise specification of $\Phi(X(T))$ may not be important. If the modeler is specifically concerned with time constraints, however, as might be the case for studies of migration, diapause, the timing of breeding activities, and so on, then careful estimation of $\Phi(X(T))$ may become important.

Ideally, T would be identified with the end of the individual's possible reproductive life span, in which case $\Phi(X(T)) = 0$ by definition. The model would then encompass the entire life span and be correspondingly more complex than a model of behavior over a limited time period. The method of "sequential coupling" (Mangel & Clark 1988, p. 69) allows one to break up the task of modeling behavior over an entire life span into more manageable submodels over briefer periods. For example, models of alternating breeding and nonbreeding seasons can be linked together.

To understand sequential coupling, suppose that a model covering the time period from T_1 to T_2 has been constructed and solved. Then $\Phi_{T_1}(X(T_1))$, obtained from this model, represents the individual's expected future reproduction from time T_1 on. This function is therefore the "terminal" fitness function for a model covering a period from T_0 to T_1 . The two models may have different environmental parameters, consider different types of behavior, and even use different units of time. In any case, the two models are linked, or sequentially coupled, by virtue of the fact that the initial fitness function Φ_{T_1} of the later model equals the terminal fitness function for the earlier model. Any number of such models can be linked sequentially; for example, this procedure is useful for modeling alternating days and nights (McNamara et al. 1987), or alternating seasons.

Backwards induction. The dynamic programming algorithm operates backwards in time from some specified terminal horizon T . This procedure may seem highly artificial. The method becomes less mysterious if one realizes that whenever behavior is considered as a dynamic phenomenon, the future becomes fully relevant. Every behavioral act has inevitable implications for the individual's future, so that the full implications of behavior cannot be understood by looking only at the immediate present. In spite of its uncertainty, the future must always be anticipated; the dynamic programming algorithm makes this mathematically explicit. Solving

backwards in time is not artificial; on the contrary it is absolutely unavoidable in any evolutionary theory of behavior.

The assumption of a fixed, known terminal time T may also appear unsatisfactory. But every individual has a maximum possible lifespan, and in a full-life model T can be equated to this maximum lifespan. The possibility that the individual dies before time T is covered by allowing for mortality risks. In a one-season model, T would represent the end of the season. In this case T may be uncertain, rather than a fixed constant. This eventuality is easily dealt with, however: One simply defines T as the last possible date in the season, and includes a probability factor for the actual end of the season at any date t prior to T .

Another possible misconception is that dynamic programming does not consider the influence of past events on current behavior. But past events affect state variables (which may include memory-related variables). The optimal behavior a^* at time t is a function of the current state variable $X(t)$, and is therefore fully responsive to past events through their effects on the individual's current state.

Reproduction. None of the models described by Houston & McNamara included reproduction explicitly; several commentators concluded that the method could not encompass reproduction. This is simply not the case, although I too have until now ignored reproduction during the modeling interval, for simplicity of presentation. Suppose now that (as shown in Figure 1) behavior in period t leads to immediate reproduction $R = R(X(t), A(t), w(t))$. Thus reproductive output may in general be affected by the individual's state and behavior, as well as by external stochastic events $w(t)$. By repeating the discussion leading to Equation (9), it can be seen that we now obtain

$$\Phi_t(X) = \max_a E_w\{R(x,a,w) + \Phi_{t+1}(G(x,a,w))\} \quad (10)$$

The interpretation of Equation (10) is straightforward: The optimal behavior a in period t is that which maximizes the sum of current reproduction $R(x,a,w)$ and expected future reproduction $\Phi_{t+1}(\dots)$. The dynamic programming algorithm, and the logic underlying it, go through unchanged.

Additional complications may arise if current behavior affects future reproduction, but this possibility can be encompassed by introducing additional state variables. An example would involve the acquisition of territory or mates prior to breeding, in which case state variables representing territory size or number of mates would be included in the model.

The state-variable dynamic modeling framework is extremely flexible. Indeed, this very flexibility can itself be problematic; it is easy to design a complex dynamic model that goes far beyond available data. Also, computational difficulties in dynamic programming expand exponentially with the dimension of the model. These questions are discussed further in sections 7 and 10.

Testability. The idea that dynamic programming models are untestable is incorrect. When constructed using empirical data, they provide quantitative predictions that

can be tested directly against field or laboratory data. Theoretical, data-free models can be developed to generate qualitative predictions, and these can also be tested against known behavior. Empirical testability is one of the most important features of the dynamic modeling framework described here.

Dynamic behavioral models are more readily testable than it may appear. Suppose that the optimal behavioral strategy $a^*(x, t)$ has been obtained for a certain model by solving the dynamic programming equations. Substituting this optimal behavior into the equation of system dynamics

$$X(t + 1) = G(X(t), a^*(X(t), t), w(t))$$

results in a time-dependent Markov chain (or a time independent chain if a^* is stationary). By iterating this chain forward in time one can generate probability distributions of the state variable $X(t)$ over time. From this state distribution, one then immediately deduces the distribution of behavior over a population of similar organisms. The latter distribution is testable against behavioral data without requiring detailed knowledge of the actual states of organisms in the population. Mangel (1987) gives a very simple example concerning oviposition in parasitic insects, showing that wide variation in clutch sizes should be expected. This prediction agrees well with the data (Charnov & Skinner 1984).

Excessive generality. Dynamic programming models are flexible, but to dismiss the method as too powerful – “capable of proving anything” – would be to misunderstand of the role of theory in science, tantamount to refusing to use the electron microscope because it reveals too much detail. Mathematical, statistical, and experimental techniques can be, and often are used incorrectly, but banning them is hardly the remedy. The predictions derived from any model depend on the assumptions used in its formulation. If the predictions disagree with observation, the model must be rejected, and new models must be sought. The model may be completely wrong-headed, or perhaps only some of its components are inaccurate, needing to be modified or replaced. Each component should be examined for biological verisimilitude; indeed separate testing of component hypotheses may often be feasible. This sequence of model formulation, testing, modification or replacement, and testing again, is the cornerstone of scientific research.

Optimality hypothesis. Whereas it is certainly true that evolution does not always maximize fitness, proponents of the claim that fitness is seldom or never maximized place themselves in the position of having to find some novel explanation for the almost universal occurrence of behavioral adaptations in nature. I prefer to accept adaptation as a hypothesis and would be surprised by any incontrovertible evidence to the contrary.

Several of Houston & McNamara's commentators cite the matching law of operant psychology as evidence of nonoptimal behavior, without explaining why it contradicts optimality. It may seem obvious that an optimizing subject should stick to a superior alternative, once it has learned which this is, but how is the subject to know that one alternative is destined (by experimental protocol) to remain forever superior? If temporal variability of the

environment is the rule in nature, adaptive behavior would require the use of sampling strategies capable of tracking a changing environment (Stephens 1987). Sampling behavior described by the matching law has this characteristic.

Simple decision rules. Another worry of Houston & McNamara's commentators was that animals may not be able to solve dynamic optimization problems the way computers do. They may be limited to using simple decision rules. This argument is flawed in several respects:

First, decision rules are exactly what a dynamic programming model produces. No one imagines that animals actually compute these decision rules by dynamic programming – fitness maximizing behavior is selected by the evolutionary process. The strategy derived from a dynamic optimization model may conceivably be too complex for organisms to use, but unless we have some idea of the *optimum optimorum* we cannot assess the degree of adaptation that observed behavior represents.

The feeding of parasitic nestlings might be quoted as an obvious example of maladaptive behavior, but if the nesting season is well advanced by the time that the pseudoparent would be able to detect the fraud, the selection pressure for learning to recognize and abandon parasitic nestlings may be quite small. Similar arguments apply in general to the interpretation of predictions derived from optimization models (Houston & McNamara 1986). Unless the predicted behavior is significantly superior to alternatives, selection pressure favoring its evolution may be weak. Even though quantitative testing of an optimization model may be feasible, the qualitative predictions are often more interesting and informative than the exact quantitative predictions (Fagerström 1987).

The claim that animals use only “simple” decision rules begs the question of characterizing simplicity. If it can be shown that a certain simple rule performs almost as well as the more complex rule obtained from an optimization model then there is clearly no reason to expect the complex behavior to evolve. The relative effectiveness of the two rules can only be assessed on the basis of some model, however; dynamic models are particularly well suited for this comparison. At any rate, I am unable to imagine how a theory of behavior with an evolutionary basis could be constructed by restricting consideration to some predetermined class of “simple” decision rules. It is not the simplicity of behavior that usually astounds us but its complexity.

7. Data requirements and model development

Every model is a deliberate simplification of the real world. Where, then, does one draw the line in terms of complexity in designing a given model? Simple models help us organize our understanding of nature, but invariably lack realistic detail.

The data available are an important consideration in model development. Models that vastly outstrip the available data may be popular with theoreticians, but they contribute little to science.

Even a simple behavioral model will often include

some parameters for which the necessary data are incomplete, however. One of the main purposes of modeling is the quantitative testing of novel hypotheses, which often means that the appropriate data have never been collected since their relevance was unsuspected. With reasonable guesses for unknown parameters one can complete the model and see whether it gives interesting and reasonable predictions. If so, the necessary data should be sought.

Many models are probably best abandoned at this early stage. If the model shows promise, however, it may be tentatively accepted as a "first-generation" model. The requisite experiments to estimate parameters and test its predictions may be designed and performed. During this process new information may come to light, and a second-generation model may be developed.

The methodology for dynamic behavioral modeling in biology is sufficiently novel that few if any such first- and second-generation sequences have yet been published. This kind of research is actively being pursued in several laboratories; I predict that such activities will expand in the future.

8. Environmental uncertainty

The dynamic modeling techniques discussed above can be extended to deal with a variety of additional phenomena, the main limitations being the availability of data and computational complexity (see sect. 10). For example, an external environmental state variable $Y(t)$, as in Figure 1, can be included. This is relatively straightforward, provided one assumes that the individual always has complete information about the environment before making any behavioral decisions. A much more interesting and difficult situation arises when the individual's knowledge of its environment is imperfect, which will often be the case in fluctuating environments.

Under these circumstances, the individual's state variable $X(t)$ can be expanded to include the current informational state about the environment. The current behavioral decision then depends on the individual's physiological and informational state variables but not on the current environmental state directly. Here we enter into the subject of dynamic decision theory under bona fide uncertainty, involving imperfect information about the present as well as the future state of the environment. Behavioral decisions must now include the possibility of deliberately sampling the environment so as to reduce this uncertainty, facilitating more effective future decisions. In spite of its obvious importance in behavioral biology, hardly any work has been done in this area (recent references include Stephens 1987; Mangel & Clark 1988, Chapter 9; and Mangel 1990). It seems to me that the biology of learning will not be well understood until this theory has been much more fully developed.

9. Dynamic game theory

Figure 1 overlooks an extremely important aspect of the evolution of behavior, namely that the behavior of any one individual inevitably affects and is affected by the

behavior of many other individuals. Thus the behavioral landscape really consists of a large collection of individual landscapes, with numerous interconnections representing predator-prey, competition, kinship, and other relationships.

Behavioral interactions have been extensively modeled using game theory, particularly the concept of an evolutionarily stable strategy (ESS) (Maynard Smith 1982); [See also Maynard Smith: "Game Theory and the Evolution of Behavior" *BBS* 7(1) 1984.] An ESS is a behavior strategy that makes the best of the circumstances, in the sense that, if adopted by the members of a population, it is not subject to invasion by a rare mutant alternative strategy. ESS models are usually somewhat difficult to analyze and tend to become much more difficult when made explicitly dynamic. The few published dynamic game-theoretic models of animal behavior have been based on strong simplifying assumptions (Clark & Ydenberg 1990; Houston & McNamara 1987; 1988b).

For example, in a model of fledgling behavior taking account of parent-offspring conflict (the offspring wishes to be pampered), Clark & Ydenberg (1990) assumed that the decisions made by the parent and its offspring alternate sequentially. This facilitated a fairly straightforward dynamic programming computation of the ESS. The model was applied to fledgling data for dovekies (*Alle alle*), a small Arctic-breeding seabird, and provided a behavioral explanation for the phenomenon of prefledging weight recession in this species. This is one of a very small number of game-theoretic models attempting quantitative predictions and may indicate a potential for the development of data-dependent ESS models.

10. Limitations

Critics and defenders of optimization modeling in biology abound (e.g., Gould & Lewontin 1979; Grafen 1984; Maynard Smith 1978; Mayr 1982; Oster & Wilson 1978; Pierce & Ollason 1987; Stephen & Krebs 1986). One can agree with the critics that the adaptationist paradigm has often been carried to extremes, and that evolution is at best an imperfect optimizer, while at the same time accepting the fact that optimization models – and their relatives, game-theoretic models – can be extremely useful in organizing our understanding of observed phenomena. Many recognized limitations of traditional optimization models of behavior succumb completely to the dynamic modeling framework described in this target article.

Indeed, the flexibility of dynamic state-variable models may itself become a source of trouble. The temptation to construct exceedingly complex dynamic behavioral models, naively thought to capture the "real complexities" of nature, could lead to a plethora of incomprehensible models, as has already happened in areas like systems ecology. It is always hard to prevent people from misusing powerful scientific techniques that they don't understand (think of statistics!).

The curse of dimensionality. Dynamic optimization theory has its roots in the calculus of variations, developed in the 18th and 19th centuries by Euler, Lagrange,

Weierstrass, and other mathematicians. The requirements of modern technology, particularly communications and space exploration, led to the reformulation and extension of the classical calculus of variations in terms of optimal control theory (Pontrjagin et al. 1962) and dynamic programming (Bellman 1957). These methods, which are now routinely applied in many fields, including engineering, operations research, and economics, have been further enhanced by the spectacular increases in computing power that have occurred simultaneously. It was inevitable that these developments would eventually affect behavioral biology.

In principle, dynamic programming and optimal control theory are capable of encompassing arbitrarily complex dynamic decision problems. Practical limitations are reached quite rapidly, however, as the dimensionality of the state space increases. This so-called "curse of dimensionality" (Bellman's term) is not a feature of any particular modeling approach or algorithm but is an intrinsic characteristic of dynamic optimization problems with many state variables.

The difficulties are twofold. First, model identification (choice of functional forms, estimation of parameters, etc.) obviously becomes more difficult as the scope and complexity of a model increases. There may be tradeoffs between a model's degree of realism and the ability to identify the model from available data (Ludwig 1989).

Second, computational requirements in terms of memory and numerical calculations increase as n^m , where m is the number of state variables and n the number of discretized values used to represent each state variable. For m larger than 4 or 5 these requirements begin to exceed the capacity of large computers. These limitations are particularly relevant for models including environmental uncertainty, since now the informational state must also be included, significantly increasing the dimensionality and complexity of the model. Similar problems arise in ESS models of pairwise contests, since the state variables of both contestants must be included.

The curse of dimensionality necessarily arises in any attempt to solve dynamic optimization, or dynamic game models. These problems are inherently complex (unless they are of low dimension); no revolution in optimization theory is likely to overcome this fact. An intriguing possibility is to use the computer to emulate the evolutionary process in searching for optimal or ESS strategies via a process of natural selection, but to my knowledge this has not yet been attempted.

The characterization of fitness. In this target article I have assumed that an organism's fitness is adequately described by its total expected lifetime reproductive output. It is well known that this definition is not always appropriate, particularly for growing or age-structured populations, or for populations in stochastic environments (Cohen 1966; Levins 1968; Stearns 1976). One adjustment, replacing the arithmetic mean with the geometric mean, is easily accomplished (Mangel & Clark 1988, p. 240), but combining behavioral and population genetic models in general would appear a daunting project (see Yoshimura & Clark in press). Grafen's (1984) discussion of the "phenotypic gambit" in behavioral modeling is relevant to dynamic as well as traditional static optimization models.

11. Conclusion

The functional analysis of behavior is by definition based on the Darwinian paradigm of natural selection according to survival and reproduction. Since these processes transpire over time, it follows that the time dimension must somehow be taken into account in any such analysis. Simplifications may sometimes be adopted so as to finesse the time dimension, but timeless models have narrow limitations which preclude the analysis of many important aspects of behavior.

Dynamic optimization techniques are significantly more difficult than static methods. Recent experience with dynamic programming models of behavior, however, has indicated many advantages for this approach. The restrictive assumptions (linearity, convexity, determinism) underlying such alternative techniques of dynamic optimization as optimal control theory become irrelevant when optimal strategies can be deduced via numerical computation. Dynamic programming models are extremely flexible and can be used to study an almost unlimited variety of behavioral phenomena. State variables and model parameters have operational significance, so that empirical testing of a model's predictions is feasible.

More important, the dynamic approach to behavioral modeling provides a completely different outlook on behavioral theory, compared, say, to the traditional models of foraging theory (see Fantino & Abarca 1985), or to models based on economic concepts like utility or indifference contours (see Rachlin et al. 1981). The entire manifold of tradeoffs ("costs and benefits") typically associated with any behavioral decision can be conceptualized and modeled in a consistent and unified way. Dynamic programming models are a natural extension of the accepted approach to the modeling of life-history traits (Horn & Rubenstein 1984).

It is only to be expected that a modeling framework so capable of encompassing realistic complexities will have practical limitations. The art of modeling consists in finding a happy compromise between simplicity and complexity which will enhance our understanding of nature.

When should dynamic as opposed to static or averaging models be considered in behavioral theory? Quantitative models are by nature less general than qualitative ones; this should be taken into account in choosing the modeling framework. My experience in behavioral modeling suggests that the possibility of designing a dynamic model should be thought about whenever quantitative predictions and testability are desired, or whenever the trade-offs between different behavioral options are of interest. None of the standard simple models of behavioral ecology have stood up particularly well to quantitative tests (Stephens & Krebs 1986, Chapter 9), although their success in providing qualitative insights should not be underrated.

ACKNOWLEDGMENTS

Alasdair Houston, Marc Mangel, John McNamara, and Ronald Ydenberg sent me their detailed comments on the first draft, leading to a thorough revision; I thank them heartily. The final draft took advantage of the suggestions of several BBS anonymous referees. My research is supported in part by an NSERC (Canada) grant 83990.

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Dynamic models of behavior: Promising but risky

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In his target article, Clark presents both the strengths and the weaknesses of a promising dynamic state-variable model of behavioral adaptations. Although he is careful to point out that such models are inherently limited by the complexity of ecological systems, we are left wondering just how useful dynamic optimization models can be. Moreover, such models pose a greater risk of misguiding theory and research than Clark's paper suggests.

Mathematical models of complex phenomena typically produce predictions and conclusions that err, to some degree, in a quantitative fashion. Quantitative errors are certainly to be expected for dynamic models of behavior, particularly because the functional contribution of any behavior can be evaluated only within an immensely complicated ecological context. Having forewarned us of the difficulties of producing models that make satisfactory quantitative predictions, Clark ends his article with the admonition not to *underrate* the ability of models in behavioral ecology to provide qualitative insights. I encourage behavioral ecologists not to *overrate* the ability of dynamic models to provide qualitative insights. Faulty assumptions, poor parameter estimation, and over-simplification can all prove fatal. Some earlier mathematical models in ecology show that (simplified) models of ecological processes can lead to serious **qualitative** errors. As a prominent biologist said, mathematicians need to avoid "developing biological nonsense with mathematical certainty" (Slobodkin 1975).

The mathematical treatments of competition provide a good example of such pitfalls in mathematical models. One potential pitfall consists of starting from false assumptions. Until recently, "virtually all mathematical treatments of competition" assumed competitive equilibrium (Wiens 1977), yet true competitive equilibrium occurs rarely, if at all, in nature (Alley 1982; Pianka 1976). The simplifications required to construct tractable models introduce additional perils. Classical competition models adopted such simplifications as stability in environmental conditions and limited genetic variation. The resultant models predicted the eventual extinction of one of two competing but coexisting populations, thereby supporting the influential principle of competitive exclusion. Moreover, lab experiments with simple homogeneous environments have demonstrated competitive exclusion (Hardin 1960). Modest changes in the models, however, indicate that coexistence of competitors may be possible (Vandermeer 1975), as field biologists believe (e.g., den Boer 1980). In retrospect, it is clear that neither the artificially simple laboratory studies nor the corresponding competition models actually generalize to natural communities (nor should they be expected to).

The newer, more sophisticated dynamic models advocated by Clark (target article) and Houston and McNamara (1988) are much less likely to make fatal assumptions about stability in environmental, genetic, or behavioral conditions because the interrelated changes in these state variables are directly incorporated in the models. Furthermore, it appears (cf. Clark's

Equation 1) that dynamic models will follow the rule that adaptedness must always be assessed in the context of an explicit environment (Slobodkin & Rapoport 1974). Dynamic models also allow the environment to be defined in terms of the functional characteristics of organisms, as must be done to capture the fundamental ecological characteristic of mutual compatibility between organisms and their natural environments (Alley 1985). Nonetheless, serious qualitative errors may arise from the processes of simplification, variable selection, and parameter estimation required by dynamic modeling.

Viable models of behavior require careful attention to ecological details (Houston & McNamara 1988) and even then may fail completely. The act of consuming a resource can be used to illustrate this difficulty.

It is reasonable, and often correct, to assume that consuming a nutritious food resource will usually make a positive contribution to an organism's fitness. Hence a modeler of behavior may estimate some *positive* value of this behavioral act, and laboratory experiments may support the model. Nonetheless, the resultant model may provide a highly distorted picture of the contribution to fitness made by a tendency to seek and consume this resource. For instance, if consuming this resource will result in potentially lethal exposure to a predator or harmful interactions with a superior competitor; the act of consuming this item may have a *negative* value. Energy costs, resource scarcity, water reserves, and many other factors influence the value of this behavior (Houston & McNamara 1988). In short, the value of this act, like almost any other behavior, may easily be misjudged.

In conclusion, dynamic behavioral models have (potentially) sufficient breadth of applicability and power to be useful in behavioral ecology. Their development forces modelers to specify precisely the most important state variables and the dynamic changes in state across time; this may prove to be a helpful guide to research. These models may provide a good way to test our understanding of behavioral ecology, but they are not to be trusted without substantial empirical support from field investigations. They may provide insight into optimal behavioral strategies, the nature of differences between taxonomic units, and ecological relationships, but are likely to yield only an approximation of true optimal behavior. I wholeheartedly agree with Clark that the modeling needs to be treated "as a process of successive approximation to . . . nature," with the models themselves continually tested against data from laboratory and field studies.

Learning and incremental dynamic programming

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It would be surprising if a computer scientist interested in the adaptive behavior of both natural and synthetic systems were to find significant grounds for criticizing the approach to behavior modeling described in Clark's target article. Optimization theory has unquestioned utility in the design of synthetic adaptive systems (with fruitful debate centering on *what* to optimize and how best to do it), and the concept of a dynamic system's state has proven to be one of the most powerful in modern engineering. Indeed, it is surprising to me that the theoretical framework described by Clark has not been more widely adopted by behavioral scientists. The complexity of animal behavior demands the application of powerful theoretical frameworks. The point of my commentary is to suggest that beyond its role in evolutionary biology, the dynamic modeling technique de-

scribed by Clark can also provide an approach to modeling animal learning at the mechanistic level.

Clark indicates that the dynamic modeling techniques he discusses are highly relevant to the biology of learning. If an animal's internal state includes information about the animal's current knowledge of its environment, then dynamic programming methods can be used to generate decision rules that take into account the utility of gathering information in the same way that they take into account the utility of gathering food. I agree that this is an important area of research that has not yet been developed (although the statistics literature contains relevant work; see, for example, Berry & Fristedt 1985). Dynamic modeling techniques and dynamic programming, however, can contribute to our understanding of learning in ways not suggested in the target article.

Clark says "no one imagines that animals actually compute . . . decision rules by dynamic programming – fitness maximizing behavior is selected by the evolutionary process." But some of us do imagine that animals actually use methods that incorporate principles of dynamic programming to adjust behavioral strategies while they are behaving. I wish to bring to readers' attention a growing body of research in which learning tasks are modeled as dynamic optimization problems and the learning system itself is engaged in a kind of dynamic programming. Instead of computing behavioral strategies that maximize evolutionary fitness, however, the learning system uses dynamic programming principles to adjust behavioral strategies to improve the total amount of "payoff" that can be accumulated over time. Payoff can be thought of as a measure reflecting the learning system's preference ordering over combinations of environmental states, internal states, and behavioral acts, to use Clark's terminology. The means by which circumstances generate levels of payoff are "hard-wired" by an evolutionary process, but a behaving system can adjust the details of its behavioral strategy to improve payoff yield over time.

From an engineering perspective, the learning problems treated according to this view are adaptive optimal control problems in which the complexity of the system to be controlled and a lack of complete prior knowledge about its dynamics prevent the prespecification of an optimal, or even useful, control rule. Unlike most mathematical formulations of learning tasks (such as those widely adopted in the field of artificial neural networks), this formulation encompasses tasks in which the consequences of an action can emerge at a multitude of times after the action is taken, and both short-term and long-term consequences must be considered in generating control actions.

On the surface, however, because it proceeds backward in time, dynamic programming would appear to be a very poor candidate for modeling learning mechanisms that operate in real time. How can dynamic programming be accomplished by a learning system unless it uses large data structures and extensive off-line processing, that is, unless it is "able to solve dynamic optimization problems the way computers do"? In addition, dynamic programming seems irrelevant as a learning procedure because it requires a detailed knowledge of the system's dynamics, knowledge not directly available to the learning system.

These properties do rule out a literal form of dynamic programming as a model of real-time learning, but there are simple rules for updating memory structures during behavior that can approximate incrementally what would be computed by a literal form of dynamic programming. In addition, such rules can do this without complete knowledge of the underlying dynamic system. These rules are based on the same recursive relationships exploited by dynamic programming, but these relationships are applied during behavior. If a learning system can experience varied and repetitive interaction with a dynamic environment, it can incrementally approximate the results of dynamic programming while always going forward in time. Moreover, the learning rules allowing this are not much more

complicated than other incremental learning rules that have been put forward as models of animal learning, for example, the Rescorla-Wagner model of classical conditioning (Rescorla & Wagner 1972), or rules used in synthetic systems, such as the Widrow-Hoff rule (Widrow & Hoff 1960).

The study of on-line learning methods for approximating the results of dynamic programming has been directed both toward designing synthetic systems and toward modeling animal learning. The use of these methods has been called "heuristic dynamic programming" (Werbos 1977; 1987) and "incremental dynamic programming" (Watkins 1989). The "temporal difference" (TD) methods analyzed by Sutton (Sutton 1984; 1988) and used in some adaptive control experiments by Barto et al. (1983) are examples of this class of method. Models of animal learning which use principles of dynamic programming include the TD model of classical conditioning of Sutton & Barto (1987) and the model of Klopf (1988) and Klopf & Morgan (in press). The TD model provides an account of a range of classical conditioning phenomena with a simple learning rule based on incremental dynamic programming. Further discussion of these ideas, their history and relation to dynamic programming, as well as references to other relevant research, are provided by Sutton & Barto (in press) and Barto et al. (in press).

As this approach to animal learning develops, its appeal to optimization theory is likely to become even more controversial than is the appeal to optimization theory in behavioral ecology. If anything, justifying a specific definition of "payoff" for a learning task is more problematic than defining evolutionary fitness, and the canonical example of nonoptimal behavior – matching behavior in operant conditioning – more directly concerns learning than evolution. I would suggest, however, that, to paraphrase Pope, a little optimization theory is a dangerous thing. In engineering design, performance criteria must either reflect what the designer really wants, or their optimization can yield totally unsatisfactory results (a point emphasized by Norbert Wiener (1964) by reference to Goethe's poem *The sorcerer's apprentice*). In a theory of behavior, explanations in terms of optimization criteria that do not reflect the true complexity of a task are inadequate and misleading. Significant progress in understanding learning can be made by adopting optimization criteria that take into account internal and external states, system dynamics, and the temporally extended nature of behavior.

ACKNOWLEDGMENTS

I wish to thank John Moore and Dorothy Mammen for helpful evaluation of drafts of this commentary.

Gaps in the optimization approach to behavior

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Although the target article is a clear and succinct exposition of dynamic modeling, the applicability of this approach is not as general as Clark maintains. The purported comprehensiveness of such modeling is symptomatic of the narrowness which would make ethology a one-legged monster (Dawkins 1989). These failings can be seen by focusing on the methodological basis of the approach, the rule of phylogenetic and developmental constraints, and the issue of mechanisms.

Contrary to Clark's assertions (sect. 1), the optimization approach may serve more to canalize, rather than organize, our explanations of animal behavior. Clark adopts the hypothesis of optimal adaptation as axiomatic based on many undisputed supporting examples. This stance is quite different from that

taken by Lande and Arnold (1983) in their evolutionary models. They note that the population mean may differ substantially from the optimum, even if an optimal phenotype exists, because of selection acting on correlated traits and hence resulting in maladaptation of the mean phenotype. Lande and Arnold conclude that only when models take such correlated effects into account will we know how frequently maladaptation of the mean phenotype occurs in the population. For his part, Clark sets up a false dichotomy by implying that critics of the optimality approach with its assumption of adaptation are forced to accept some novel process of evolution other than natural selection.

The dynamic modeling described by Clark is most useful when the traits in question are directly under selection pressure. It is not clear how Clark can make this a universal assumption rather than an open question in need of empirical verification. For example, he gives an optimality-type argument to explain the lack of a selective response to the feeding of parasitic nestlings by pseudoparents (sect. 6, Simple decision rules) even though such arguments have already been shown to be incorrect (Rothstein 1982; 1986). Rothstein (1982) sees the heuristic value of optimization models but urges that less certainty be attached to the notion that animals always behave in an adaptive fashion. The lack of an adaptive response to brood parasitism by some species illustrates that heritable variation in specific traits cannot be taken for granted. This is especially true for traits associated closely with fitness, which can go quickly to fixation (Falconer 1981). Brood parasites have presumably capitalized on just such a strong selection response for parents to feed offspring in their nest (Jamieson 1989a).

Phylogenetic and developmental constraints of this type illustrate the second major limitation of optimization models. Constraints are implicit in optimization and history is implicit in adaptation. However, Stearns (in press) has argued that history enters optimization models only in a superficial way. When theorists build optimization models, they assume certain trade-offs. Trade-offs differ significantly among lineages, but optimization models applied to different lineages simply assume the relevant constraints without asking why they have changed: "one just notes that they have, incorporates them into the analysis and having used them, perhaps to make a successful prediction, forgets about them." What is missing in an optimality approach is an understanding of why important constraints differ from lineage to lineage. The study of function and of evolution of behavior are interactive, not separate, problems (Jamieson 1989b).

Clark's approach also cannot specify, or even suggest, mechanisms in specific behavioral situations, whether the anticipation of the future (sect. 6, Backwards induction), matching behavior (sect. 6, Optimality hypothesis), the structure of decision rules (sect. 6), the biology of learning (sect. 8), or the general problem of behavioral patterning. As Ollason (1980a) has pointed out, mechanisms can be interpreted in terms of function, but the reverse is not true. For these problems, such other approaches as that of Fantino and Abarca 1985 (sect. 11), are not only possible but essential.

Under an optimization approach, when modellers need to make assumptions about how animals assess things such as each others' size, territory quality, and parasite loads, they generally cannot support them. Dawkins (1989) has argued how much more impressive optimal foraging models would be if we knew which assumptions (about memory and perception) were realistic, which were unlikely, and which were contrary to everything that was known about animal vision and memory. What Clark fails to note is that evolutionary models of behavior need a mechanism just as much as the study of mechanisms needs an evolutionary perspective.

One serious problem that arises from the lack of emphasis on behavioral mechanisms is that predictions from mathematical models can be supported when the actual mechanism assumed to be operating in a model is wrong. Bell (in press) illustrates this

point with an example from optimal foraging. Using an optimal foraging model, Pyke (1978) predicted that bees should stay in a patch of highly rewarding flowers, pass quickly through a patch of low-reward flowers, and not forage at all in a patch of empty flowers. In testing this hypothesis, Pyke found that his predictions about the mean angular deviation between arrival and departure was supported. To explain the results, Pyke developed a rather complex set of departure rules for bees in a rewarding patch. As summarized by Heinrich (1983), to accomplish this feat a bee must remember, before computing a new departure angle, not only the direction it came from each time it visits a flower but also the rewards of previously visited flowers and previous departure directions. In fact, what happens is that the bees simply turn several times around on a rewarding flower, contributing to the predicted randomness in their take-off direction.

Optimal foraging theory may have generated a useful functional model of behavior, but it led to a totally inappropriate hypothesis of the proximate mechanism involved. Dynamic models could be subject to the same problem. It is relatively clear what must be done when the predictions of a particular model are not supported, but Clark does not recognize that Type II errors may be relatively common in a mathematical approach that pays little attention to biological details.

Dynamic programming, limited information and behavioral modeling

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Clark's target article provides some persuasive arguments about the importance of using dynamic models in a variety of quantitative studies of behavioral processes that have presumably been shaped by natural selection. From the perspective of "traditional" applications in which dynamic programming models have been successfully used, it is a familiar approach to start by specifying a difference equation to describe a family of state-space paths parametrized by a sequence of admissible control or decision variables, and by formulating a reward criterion whose maximization produces a sequence of optimum decisions and the corresponding optimum performance. For a comprehensive treatment of dynamic programming, see Bertsekas 1987.

The problem of obtaining suitable mathematical formulations of the difference equations and reward criteria describing complex biological systems is a challenging one, but it is hardly unique to this application; for example, the same problem is faced in many applications to economic systems. Indeed, for both kinds of applications there is little reason to assume the existence of an underlying "true system" described exactly by a model of the form used in behavioral studies. Mathematical models that involve plausible relationships between variables and that accurately approximate behavioral characteristics provide a way to expose structure and to help explain it. When plausibility is sacrificed for the sake of simplicity or tractability, the resulting model takes on a greater level of empiricism, and its explanatory power can be expected to decrease.

These general comments set the stage for my critique of Clark's article. It is my contention that the issue of *limited information* must be incorporated in the description of dynamic programming in order to maintain the plausibility of the basic model. When a dynamic programming model includes a restriction on the functional form of control inputs arising from an explicit specification of the available state information, the fundamental nature of an optimum behavior is strongly affected. In the case of *full information*, the entire state vector is available

at each stage and optimum control inputs depend only on instantaneous state values. In the case of partial information, however, optimum control inputs depend on the entire past history of observations. Only in rare cases will there exist a finite dimensional *realization* of the optimum controller; in other words, any controller with "fixed memory size" is necessarily suboptimal. See Bertsekas 1987, Chapter 3.

There is also some evidence that the difficulties caused by limited information in dynamic optimization problems extend beyond the framework introduced in Clark's paper. In the case of behaviors that can be modeled by *discrete-event systems* rather than by difference equations, it has been shown that some dynamic optimization problems involving partial information are intractable in the sense of computational complexity theory (Tsitsiklis 1989).

The issue of limited information is not completely ignored by Clark, who briefly mentions it in section 8 in connection with modeling environmental uncertainty. The importance of dealing explicitly with limited information is much more basic, however, and hence more important. The model for fledgling behavior used as an example in section 5 can also be used to illustrate how limited information relates to the modeling process. The model's state vector $X(t)$ includes $W(t)$, the chick's weight, as its first component. There is a two-parameter nestling growth function $g_0(w)$, and there is a similar growth function $g_1(w)$ valid after fledging. A weight-dependent reward function is also introduced. The resulting optimal fledgling behavior is given in Table 1. Let me pose two basic questions. First how does a chick know its weight? Second, what is the effect of parametric uncertainty in the descriptions of the growth functions? These questions are posed not to challenge the usefulness of the model, but to raise flags about two basic issues concerning dynamic programming with limited information.

As suggested by the first question, it is often not plausible that the quantities comprising the state vector of a dynamic model are all available for measurement. State estimates based on the limited information available may need to be incorporated as part of the optimum behavior. Of course, in models where a state variable plays a surrogate role (as above, where weight is an external manifestation of some internal metabolic variable), this need not be a case of limited information.

The second question concerns a generic issue. If we assume that the form of the difference equation used to describe the state dynamics (or some alternate form for specifying allowable behavioral data) is genetically programmed in each individual, then to achieve optimum behavior while allowing for parametric uncertainty requires a dynamic programming formulation involving limited information. Unknown parameters must be included as components of the state vector; even though the dynamics of these quantities are trivial (constant over time), the fact that the parameters are not directly observed is a crucial difference because the resulting model involves partial state information.

What is the point of emphasizing limited information in the context of dynamic programming models of behavior? My answer is that it adds plausibility in at least two different ways. First, partial state information becomes more and more realistic as the complexity (and accuracy) of dynamic behavioral models increases. Second, partial state information allows for parametric uncertainty in dynamic models, thus making it more realistic for natural selection to express optimum behavior.

The occurrence of adaptivity in Nature's implementations of biological behavioral control processes supports indirectly our view of the importance of limited information. Standard approaches in conventional applications of dynamic programming include *certainty equivalence*, where the models obtained by assuming full information are modified to incorporate estimates of unobserved quantities, *open loop feedback control*, where the effects of future measurements are ignored in determining control inputs, and various other forms of parametric adaptive

control. Chapter 4 of Bertsekas 1987 provides more details. Adaptive systems presumably also cope with "unstructured uncertainty" (e.g., unmodeled dynamics) in the system models. Various manifestations of adaptive behavioral control could conceivably be examined through experiments suggested by mathematical models with partial observations.

In conclusion, the prospects for modeling behavioral evolutionary processes using tools of dynamic optimization seem bright. Clark's target article points out some of the future challenges. I have used the issue of limited information to suggest that suboptimal individual behavior arises, at least in part, from basic mathematical considerations, and that adaptive features of individual behavior are likely to be related to necessarily suboptimal implementations. Model-based sensitivity studies might also indicate situations where there are no significant performance improvements to be gained through adaptive control and so a fixed, genetically programmed "nominal controller" would be sufficient for generating the desired behavior.

Rules of choice

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Behaviorists should be indebted to Clark for his lucid and informative review of dynamic modeling. I certainly applaud his functional analysis and the potential usefulness of the modeling approach. I am particularly partial to his claims that: (1) models can be "tremendously helpful" when treated as a "successive approximation to the complexity of nature"; (2) solving backwards in time is the natural and necessary way to develop a model for an evolutionary theory of behavior; (3) optimal behavior is entirely responsive to past events.

Clark takes some of Houston & McNamara's (1988a) commentators to task for citing "the matching law of operant psychology as evidence of nonoptimal behavior, without explaining why it contradicts optimality" (sect. 6, Optimality hypothesis). I have mixed reactions to this section, in part because it too is somewhat sketchy in explaining the author's position. Perhaps he will address these concerns in his Response. First of all, the fact that matching often occurs when it is nonoptimal cannot be dismissed so readily by an appeal to the benefits of sampling in tracking a varying environment. As Heyman and Herrnstein (1986) have shown, pigeons may evince matching rather than optimal behavior after many many hours (in daily sessions taking place over several weeks). Their tendency to match does not diminish over extensive exposure to the nonchanging environment. More important, the pigeons do not follow a maximizing strategy with occasional deviations to sample (a pattern consistent with the interpretation presented); instead, they follow a matching strategy which precludes maximizing.

It is true, however, that matching and maximizing are usually equivalent. Thus, matching may be one solution pigeons have developed for generating choice behavior that is generally optimal. As a second example, consider delay-reduction theory (DRT), developed in the operant choice laboratory and applied to foraging decisions (e.g., Fantino 1969; 1987; Fantino & Abarca 1985; Fantino & Preston 1988; 1989). As shown by Fantino and Abarca, DRT is equivalent to the optimal diet model of classic optimal foraging theory. However, situations may be constructed so that the predictions of DRT differ from a model maximizing food availability over time. Specifically, according to DRT, hungry subjects should choose the outcome correlated with the greater reduction in time till the next opportunity to eat over an alternative correlated with slightly less delay reduction but with a greater overall rate of food

availability. Wendy A. Williams and I are demonstrating that in such cases pigeons strongly prefer the outcome with greater delay reduction. Again, as I suggested with respect to the matching law results, it may be that rules such as delay reduction lead to sufficiently optimal outcomes so that they become the rules of choice. Such cases of nonoptimal "satisficing" rules may also help explain otherwise anomalous phenomena in human behavior (e.g., illogical behavior, see Nisbett & Ross 1980).

What remains unclear to me is how these types of adaptation – including sensitivity to matching and to delay-reduction – are accounted for by the dynamic modeling framework described in the target article. Clark is perhaps suggesting an answer when he writes: "Unless the predicted behavior is significantly superior to alternatives, selection pressure favoring its evolution may be weak" (sect. 6, second last para.). However, a more complete account is needed if the dynamic modeling framework is to encompass choice behavior comfortably.

ACKNOWLEDGMENT

Preparation of manuscript supported by NIMH Grant MH-20752.

Can dynamic optimization cope with ecological complexity?

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Introduction. Ethological and ecological studies use the expression "causal explanation" in two different senses. The expression may mean the longterm processes of natural selection of traits which confer a certain "fitness" on their carriers. This is the "evolutionary" or "teleonomic" explanation. On the other hand, ethologists use the term "cause" to refer to short-term determinants of a behavioural act. The latter factors are termed behavioural "mechanisms," and the complex set of interactions that link the individual to its environment are termed "behavioural mechanics." In this commentary, to avoid confusion with dynamic programming, I will not use the term "dynamics" (*sensu* dynamics in physics) for these processes.

Despite the evident logical affinities between the two kinds of causes, they are studied with methodologies that differ so much that the reciprocal links remain undetermined in most studies. In general, behavioural "mechanistic" studies refer qualitatively (and often uncritically) to the adaptive value of the behaviours studied.

Optimal foraging theory (OFT) has introduced a new approach in behavioural studies, explaining long-term phenomena in terms of short-term processes. In fact, its main assumption is that short-term behavioural optimisation produces "fitness maximization." In other words, OFT explains evolutionary patterns in terms of behavioural adaptations (cf. Clark's discussion about the computation of lifetime reproductive outputs). The long-term determinants remain important even when nonadaptive processes of evolution (e.g., drift, dispersal, etc.) are taken into consideration. Accordingly, OFT models' predictions can be tested directly against experimental or field evidence.

"Classical" deterministic models of OFT (Stephens & Krebs 1986) predict average individual behaviour. By contrast, dynamic optimisation can inform us about the time evolution of behavioural patterns, with a temporal definition that depends only on the power of the computer used. If Popperian refutability is the chosen scientific standard, these fine-grained predictions of animal behaviour confer a more elevated epistemological status on stochastic optimisation compared to "classical" OFT deterministic models.

Clark states (sect. 6, Excessive generality) that a "sequence of

model formulation, testing, modification or replacement, and testing again, is the cornerstone of scientific research." This is undoubtedly true, but it is necessary to be aware that this sequence depends critically on the efficiency of the testing procedure. The quality of the testing procedure is of the utmost importance especially when field data are used. Most OFT reviewers (e.g., Stearns & Schmid-Hempel 1987) are worried that a wrong model may be accepted as a consequence of the smallness of the sample sizes (implying high standard errors of the estimates) that are used in many tests (type II statistical errors). The aim of this commentary is to call attention to the other possible error (type I risk), that of rejecting a good model. Following the "sequence" described above the rejection of a good "simple" model may lead "to a plethora of incomprehensible models."

Behavioural mechanics and optimization models. An animal that would want to adopt an optimal strategy may not be able to follow it, and may be obliged to shift to the best nonoptimal strategy available.

Under natural conditions a certain number of factors may influence the performance of an animal that is following an optimal policy:

1. The optimal action is physically impossible. Suppose we are studying the group size selection process, and let m^* denote the optimal group size for an animal characterized by a certain value $X(t)$ of its individual state. A group of size $m^* - 1$ may not be present in the environment so that the optimal action cannot be performed. In this situation, the animal's optimal choice is to select among available groups the one which yields the largest fitness. In addition, a large herd may split if there is a fitness advantage. Accordingly, one may expect to find under natural conditions herd sizes that exceed optimal values, an upper bound being the lowest size m for which the individual "expected fitness" in a herd of size $m/2$ exceeds that in a herd of size m (an overflocking situation; cf. Clark & Mangel 1986).

2. The optimal action may be performed with delay. For example, when the animal has to select a habitat from a set of possible ones, it may happen that some time is lost before it reaches the right one (see the example in Houston et al. 1988).

Similar arguments may be developed for numerous other "disturbing" factors.

Discussion. With respect to predictions of dynamic optimisation, the test of "static" models – when large data sets are used – may be significantly affected by the disturbing factors discussed above because the effect (i) simply increases the variance of the estimate, while the mean value may asymptotically converge to m^* , whereas the effect (ii) is ignored. In any case, the amount of unexplained variance would be large.

The argument presented here is not meant to support the claim that optimisation is impossible or that when it exists it is unmeasurable. The aim is only to show that a simple direct statistical comparison between the field observations and the models' predictions may yield significant differences even when the modeling assumptions are correct.

I have stressed here that this kind of problem arises when field data are used. In a laboratory approach, a clever experimental design may strongly reduce or even eliminate these difficulties. In the case of the detailed predictions allowed by dynamic optimisation, ignorance of the underlying behavioural mechanics may be quite critical. Models and simulations of an animal's movements in relation to habitat structure (including interactions with conspecifics, predators, etc.) represent the logical interface between optimisation models and the real world. If mechanistic models are not introduced in the testing procedure, there is a concrete risk of developing optimisation models that are too complex and are subject to an excessive number of constraints. In the face of computational difficulties, complex models lose their heuristic value by diluting the key elements among a large number of ad hoc hypotheses.

The approach suggested here recovers many of the the-

oretical results about the behavioural bases of foraging and social behaviour that have been in part neglected by the most recent developments of the sociobiological debate, strongly concentrated on the "why" question. In particular, I refer to the analysis of foraging paths and the formation of social groups (reviews may be found in Deneubourg & Goss 1989 and in Alt & Hoffmann 1990). A useful discussion of the relationship between mechanistic and optimality models is also presented in Ollason (1980b).

Such a unified foraging theory as the one proposed by Mangel and Clark (1986) must incorporate the two kinds of causal explanations. In my view, OFT and dynamic programming have significantly contributed to such a unified view of foraging ecology.

ACKNOWLEDGMENT

I wish to thank Professor S. L. Paveri-Fontana for helpful discussions.

Dynamic models, fitness functions and food storing

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Colin Clark has provided a clear introduction to the elements of dynamic programming, along with some eminently sensible comments on the purpose, power, and limitations of modeling in behavioral ecology. Of particular value is his emphasis on the idea that modeling is itself a dynamic activity. In the right hands, first generation models clear away the brush, stimulate a search for better empirical data, and point to gaps in our understanding of why animals behave as they do. Further models build on the information provided by earlier efforts and if nature is in the mood to yield up a few secrets, they advance our understanding. This view of modeling exposes the fallacy in Gould & Lewontin's (1979) argument that the study of adaptation is flawed because it substitutes new adaptive explanations when old ones fail. All scientific activity proceeds by substituting new explanations when old ones fail. Modeling in behavioral ecology simply introduces some rigour into the process that should be welcomed by both adaptationists and skeptics.

A few critical comments can be made about the target article. It is by no means clear that the matching of responses to reward distributions is an optimal sampling technique (sect. 6. Optimality hypotheses). Nor is it clear that understanding sampling is the key to the biology of learning (sect. 8. Environmental uncertainty). Some learning does resemble the sampling of values from a known distribution (Stephens & Krebs 1986), but much learning does not. Learning to recognize and discriminate places, objects, and events, learning contingencies between events, and the learning of motor patterns have little to do with sampling the state of the environment in the sense intended by Clark. Even if we ignore the problem of how the environment is represented and concentrate on the functions of learning, the importance of sampling is as a point of contact between optimality modeling and learning theory, not as the essence of learning. These issues are not the main thrust of Clark's target article, however.

More central to Clark's presentation, and to Houston & McNamara's (1988) earlier target article, are questions about the nature of the terminal fitness function in dynamic modeling. The existence of a stationary behavioral policy that is independent of the terminal fitness function and of the time to run until the final time T is reached is an intriguing property of dynamic models. Clark acknowledges that this independence holds only under certain conditions, but for the most part he argues that the problem of specifying the terminal fitness function is not

severe. When is the relative ranking of final states truly unimportant in determining the optimal policy, however? In general, how much time between t and T is required before the behavioral policy becomes stationary? Stationary policies only exist when the state and environmental dynamics remain constant for some period of time. The degree to which this property is useful depends critically on how biologically realistic a period of constant conditions is. One of the strengths of the dynamic approach to modeling behavior is the facility with which it can accommodate changes in conditions over time. When this is desired, or when we are interested in modeling behavior for t close to T , the difficulty of determining the terminal fitness function remains.

There is no question that dynamic models can contribute a great deal to the progress of research in behavioral ecology. Two recent dynamic models of food storing by birds illustrate this (Lucas & Walter, in press; McNamara et al. 1990). Storing food appears at first to be a losing proposition, because the expected energetic return on stored food can only decrease from its current value, through pilfering losses, deterioration of stored food, and failure to relocate caches. The energetic value of the food is just part of the picture, however. Indeed, stored food really has no fixed value at all to the animal because its value depends on changes in the state of the hoarder and the environment between the time of storing the food and recovering it. Food may become less available, increasing the fitness gain from having previously stored a supply of food. Food may become more available, reducing the cost of collecting food compared to usual foraging conditions, and thereby promoting storing. Energy requirements may increase because of a drop in temperature or because of breeding activity. Risk of starvation may increase or decrease depending on the animal's recent foraging history. Dynamic models seem to be the only reasonable way to capture the state dependencies that govern food storing decisions.

The dynamics of food storing can become particularly complex for a further reason. Food storing by many species, including chickadees, tits, Clark's nutcracker (no relation), other corvids, and woodpeckers takes place in social groups. Black-capped chickadees do most of their food storing in fall and winter in small conspecific flocks that are joined during foraging by nuthatches, kinglets, and woodpeckers. Food storing decisions are likely to be affected by the probability of losing stored food to other birds that see it being cached, and by the opportunity to observe and rob the caches of others. Food storing thus becomes a dynamic game in which decisions are influenced not only by the animal's state and the state of the environment but also by the behavior of others. Adequate models of dynamic games would clearly be welcomed by many behavioral ecologists.

Clark makes a number of important points about testing dynamic models. One of these, illustrated by Mangel (1987), is that a dynamic model can generate the distribution of the state variable $X(t)$ over time, and hence the distribution of behavior in the population. This predicted behavioral distribution can be compared to an observed distribution of behavior in situations where the measurement of the state variable in individual animals is impractical. The predicted distribution of food storing and cache recovery behavior, for example, can be compared to field observations without requiring a knowledge of state variables, such as body weight, for individual birds. Finally, the "curse of dimensionality" may be less of a curse than Clark supposes. A modeling technique that produces reasonable qualitative or quantitative predictions while keeping the number of variables that must be measured to a manageable number bestows the blessing of dimensionality on laboratory and field workers.

The next state of the art

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Not surprisingly, we are in agreement with the general approach based on stochastic dynamic programming (SDP) advocated by Clark. We also agree with most of the specific points that he makes. The peer commentary on Houston & McNamara (1988a) contained many misconceptions. We hope that our Response to the peer commentary and now Clark's target article will eliminate these. Rather than going over this ground again, we will concentrate on how this research field may develop.

Like any other theoretical approach, SDP can be misapplied. This is especially likely when an approach becomes fashionable. An approach should be used because it is appropriate, not because it is the flavour of the month. We are worried that the power of SDP may encourage people to analyze problems by using brute-force numerical techniques when more insight might be gained from a simpler analytic argument. As with all modeling-building, one must use judgment in deciding how to proceed. It is almost always worth exploring a simple schematic model of a system in an attempt to understand what features are important (see also Houston 1990; Smith 1988). In using a schematic model one must be aware of its assumptions and limitations. The model may capture some aspects of the problem, but because of its limitations it will be unable to capture other aspects. One may then want to make a more realistic model that requires numerical solutions. Just because SDP can solve almost any problem, it does not mean that it has to be applied to almost every problem.

Matching cannot be understood in terms of the maximization of the rate of energetic gain. Houston & McNamara (1988a) outlined some broader contexts in which matching could be favored by natural selection. Clark suggests sampling as a possible explanation. We are not convinced that the regularities in behavior that are accounted for by the matching law can be explained in this way. The topic deserves further investigation.

Because SDP works directly with survival and reproduction, it can be used to link behavior to population dynamics. Along the way one can investigate ecologically relevant issues like the relative magnitudes of starvation and predation (McNamara 1990; McNamara & Houston 1990a) and the distribution of animals between habitats (McNamara & Houston 1990b).

Dynamic games are biologically important and present many interesting theoretical challenges. We have continued our approach based on considering a large population of animals (McNamara & Houston 1990b). Clark and Ydenberg (in press) and Kelly (1989) consider interactions between a small number of animals that are able to recognise each other.

Adaptive explanations of behavior must (either directly or indirectly) relate the consequences of an animal's behavior to its life-time reproductive success. SDP provides a natural framework for doing this, but it is not the only feasible approach. An alternative is to follow the evolution of a population under natural selection, as suggested by Clark. This approach has been used by Poethke and Kaiser (1985). Sumida et al. (in press) review the use of a pseudogenetic search mechanism called the genetic algorithm (GA) in a biological context. The GA is a powerful search procedure that can find optima in very large search spaces. We see GA's as being useful in the study of problems where there are many dimensions or there are interactions between animals, as in dynamic games.

Modeling adaptation in the next generation: A developmental perspective

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Like Houston and McNamara (1988a), Clark describes a modeling technique that advances our understanding of behavioral ecology. Dynamic modeling links developmental change with an evolutionary framework; however, such modeling is not restricted to evolutionary outcomes. For example, one can model weight gain, language learning, or any number of other significant developmental adaptations in place of fitness. Thus, functional analysis can be considered a special area of developmental biopsychology.

We have argued, as Clark has, that the complexity of natural systems requires the modeling of phenomena in continuous time (Howe & Rabinowitz, in press). This dynamic perspective contrasts with more traditional state or stage conceptions of development. Although not intended by Clark, even within a dynamic framework, states can be seductive. That is, a description of an organism at a particular point in time can be misinterpreted as a semipermanent characterization. When one breaks time into discrete units, the end of each unit may be conceived as a theoretical convenience or a state of the organism. The latter idea is congruent with the recommendation that we should describe states and look for transition mechanisms between them (Simon 1962). This contrasts with the perspective that development is transition or that biopsychological models must be dynamic.

Within this broader context, as well as in Clark's discussion, it is an oversimplification to exclude environmental variables or merely relegate them to organismic states. Clearly, behavior occurs in a context, and it would seem that the virtue of dynamic modeling in the study of adaptation lies in its ability to capture this organism/environment interaction. Critical environmental contingencies (e.g., protein deficiency during infancy) markedly constrain future organismic states. Although we appreciate the difficulty in modeling the complexity of natural systems, we find it hard to imagine modeling behavioral adaptation without an environment. The curse of dimensionality may be a temporary technological impediment, but it is not a sufficient justification for ignoring a major component of the adaptive process.

Next-generation models must also confront the multifaceted problem of parameter estimation. First, the model must be identifiable. In particular, we must be able to generate unique estimates for each parameter. Second, when we have determined that the model is identifiable, quantitative predictions about empirical phenomena can be generated. In order to evaluate the accuracy of such predictions, goodness-of-fit machinery is needed. At the very least, one must be assured that the model is both necessary (parsimonious) and sufficient (adequate), that it has the fewest number of parameters needed to account for the data. Although backward propagation has been criticized as a goodness-of-fit technique, it is a commonly used regression procedure that permits (forward) prediction. In our view, backward propagation represents a useful addition to the usual collection of goodness-of-fit techniques. Developmentally, both forward and backward propagation methods will be necessary to evaluate the utility of the stage concept. Finally, having established the relevant parameters through goodness-of-fit tests, the validity of the parameters' theoretical interpretations must be assessed. Such questions are formally addressed statistically, and require operationalization and manipulation of independent variables. It is only through rigorous experimentation and statistical evaluation of changes in parameter estimates, that such validity can be established.

We close by noting that the purposes of scientific theory are to organize knowledge, generate falsifiable hypotheses, and predict new phenomena. Although such ideas as optimality have played a critical role in theory construction, they confuse the process of theory evaluation. What matters in evaluation is how well quantitative models generate an understanding of processes and outcomes. Within this perspective, mathematical equations can potentially predict behavior such as probability matching (e.g., Heyman 1988) and environmental sampling (e.g., Stephens 1987), not whether errors determine optimality. Questions about the optimality of such behavior are not falsifiable, are outside the model's domain, and only promote loose speculation and circular argument. We hope that next-generation models will be sufficiently productive/predictive that researchers will focus on developmental issues to the exclusion of definitional controversies.

NOTE

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Limits to stochastic dynamic programming

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Clark provides a useful description of the technique of dynamic programming and outlines its main advantages. His major worry concerns the complexity of models. He warns (sect. 10) of the temptation to include excessive detail and how this can lead to the sort of pointless heavyweight exercises that capsized and sank systems ecology. We think it is important to understand the real problem of producing complex models.

In his conclusion, Clark points out that the standard simple optimisation models of behavioral ecology have failed to stand up to quantitative tests, although they have provided qualitative insights. The real success of such simple models as the optimal diet model, the marginal value theorem and the ideal free distribution was that they changed the perspective of a cohort of ecologists so that they studied animals in a different way. This led directly to the recognition of the importance of components such as misidentification (Hughes 1979), kleptoparasitism (Thompson 1983), variation in prey quality (Durrell & Goss-Custard 1984), and individual differences in predator quality (Sutherland & Parker 1985).

Dynamic models will probably fail to stand up to quantitative tests also (albeit in different ways), but for the same reason it will not matter. If the technique can contribute to interest in new sorts of problems then it will have made a real contribution. It has already started to do so, as the lack of a quantitative framework in which to incorporate stochasticity, the time dimension and competing demands for an animal's attention definitely contributed to behavioural ecologists ignoring the importance of these factors in the past. Now, the importance of tradeoffs, central to all sorts of decision-making, is being widely examined both through modelling (e.g., Mace & Houston 1989) and purely empirical work (e.g., Cuthill & Guilford 1989).

Dynamic programming involves an interaction between nature, computers, and human brains. Nature is complex and computers are becoming increasingly capable of describing such complexity. The "curse of dimensionality" is as much a problem for human understanding as it is for the power of the computer. Computers have no problem handling four or five dimensions – the weak link is the human brain. It is possible to create models with more than one state variable and several behavioural options (and solve them numerically). But, in our experience, as the complexity of the model exceeds one state variable or two

behavioural options it can become increasingly hard to make sense of the output.

Clark's abstract states that "limitations arise because nature's complexity always exceeds our modelling capacity," but this is not the real problem. The major challenge is to abstract the complexities of nature in a way that will capture the imagination of its students.

Models are just prostheses for our brains

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Without using algebra we can only make qualitative hypotheses in our heads and express them in words. A mathematical model is (only) a hypothesis formulated quantitatively and expressed in numbers. There is nothing more to a model that deserves either condemnation or glorification. The model is a tool to formulate hypotheses for research when the natural phenomenon under study is too complex to be handled by the limited channel capacity of our brain. In this respect, the dynamic modeling technique is no different from other well accepted models. It allows us to put more realistic complexity into our hypotheses, but at the same time it often robs us of the excuse that it is impossible to predict a behavior quantitatively because of its complex conditions.

As an empiricist I am as happy to have this new and more powerful instrument as I am to have a new and more powerful word processing program. However, in both cases the value of the results produced with the new tool depends very much on what I am using it for. The laborious part of the job is concealed in sentences like the following (Clark's abstract, emphasis mine): "The models use *biologically meaningful* parameters and variables, and lead to testable predictions." I hope that editors keep this in mind when they soon receive vast numbers of manuscripts starting with "using dynamic programming techniques we have demonstrated that . . .".

Let evolution take care of its own

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Clark's title is somewhat misleading. Rather than modelling *behavioral adaptations* per se – specific psychological mechanisms capable of generating adaptive behavior – Clark's dynamic programming method computes specific behavioral sequences designed to optimize fitness given precalculated *adaptive pressures*. Indeed, adaptive pressures are precisely what Equation 9, the central expression of Clark's method, represents.

Yet Clark's title does point in the right direction: Behavioral adaptations *are* what we want to model. Characterizing evolved psychological mechanisms themselves is crucial to understanding behavioral responses to the adaptive pressures that emerge in complex environments, for it is at the level of mechanisms, not individual behaviors, that analyzable regularities most clearly appear. As Cosmides & Tooby (1987) argue, psychological adaptations must serve as the intermediary between adaptive pressures and behavioral strategies; one cannot take the short-cut of finding behavioral strategies directly given adaptive pressures.

The phenomenon of protean (adaptively unpredictable) be-

havior illustrates this levels-of-analysis problem. Simple proteanism occurs when a rabbit flees a fox by "randomly" darting back and forth (Driver & Humphries 1988). If the rabbit had internalized the sort of look-up table for escape behavior suggested by the dynamic programming method, always choosing the "optimal" escape route in its attempts to maximize Equation 9, the very predictability of this behavior would render it unfit. Foxes would evolve predictive counterstrategies. Suppose instead that rabbits have not simply evolved a set of behavioral strategies *per se* (as suggested by the dynamic programming method), but a more abstract, flexible behavior-generating mental mechanism that allows them to behave unpredictably in certain circumstances. Although this mechanism may violate dynamic programming optimization, perhaps causing some rabbits to perform suboptimally in the short term (e.g., zigging when they "should have" zagged), this mechanism may nonetheless increase the average fitness across the subpopulation of those rabbits possessing it. Although Houston & McNamara (1988) allude to the possibility of dynamic programming selecting probability distributions across behaviors (which would yield a kind of proteanism), the proper level of analysis here is that of the complex protean psychological mechanisms themselves. These mechanisms are the true behavioral adaptations, but ones that dynamic programming seems incapable of revealing.

More seriously, dynamic programming seems unable to adequately model the optimization of *inclusive* fitness (Hamilton 1964), rather than just *individual* fitness. With inclusive fitness, there is no specifiable final time T beyond which a behavior's effects will not propagate; because the effects of an organism's behaviors may continue long after its death, affecting its kin and offspring for many generations, there is no reasonable endpoint for assessing ultimate fitness. Thus our models of behavioral adaptations must consider fitness effects of interactions *between* individuals, both within and across generations, not just within an individual's own life-time. Dynamic programming may be sufficiently powerful in principle to represent the interaction contingencies of social behavior by breaking them down into adaptive pressures impinging on organisms considered individually. But if one tries to imagine exactly how this would work with collaborative or competitive behaviors as complex as coalitional aggression or social exchange, dynamic programming seems less than entirely efficient.

Modeling interactions with other individuals in the environment leads naturally to modeling interactions with the environment itself. This step would free us from specifying quantitative adaptive pressures impinging on the individuals. Rather, the adaptive pressures molding the evolution of behavioral mechanisms could emerge from the dynamics of the modeled environment and the fitness function defined over it.

Finally, modeling actual reproduction and inheritance directly seems simpler than representing adaptive pressures in terms of expected future reproduction or some other abstract fitness construct. The reason creatures operate in accordance with inclusive fitness is that by aiding their relatives they are aiding the spread of their own genes – their relatives are likely to have copies of their own genotypic specifications of phenotypic mechanisms. Modeling inclusive fitness without actually modeling the spread and recombination of genes just misses the point. These considerations lead us to wish for a method of modeling the evolutionary spread of successful psychological mechanisms from one generation to the next, in response to adaptive pressures emerging from a specified environment with which, and within which, individuals interact.

Clark himself suggests that "An intriguing possibility is to use the computer to emulate the evolutionary process in searching for optimal or ESS strategies via a process of natural selection, but to my knowledge this has not yet been attempted." (sect. 10, para. 7) In fact, the entire field of *genetic algorithms* (Goldberg 1989; Holland 1975; Schaffer 1989) and much of *artificial life*

research (Langton 1989) rely on computer instantiations of evolutionary dynamics to produce adaptive solutions to specified problems – often solutions in the form of neural or psychological mechanisms underlying behavioral strategies.

Our research, for example, uses genetic algorithms to simulate the evolution of neural networks that control the behavior of simple organisms in simple virtual environments (Miller & Todd 1990; Miller et al. 1989; Todd & Miller, in press). Ackley (1990) has produced a more complex and suggestive model of the evolution of adaptively behaving creatures using a similar approach. In these models, adaptive pressures are not explicitly represented, but emerge from the dynamics of the environment and the interactive behavior of the simulated organisms. In all such methods, the evolutionary process itself is the search for optimal behavioral strategies. Although no global optimum is guaranteed to exist or to be findable in finite time, genetic algorithms have generally proven superior to any other search method for very large, complex search spaces with many local optima (Goldberg 1989).

We sympathize with the desires of Houston & McNamara (1988a) and Clark to develop computational tools for analyzing the adaptive functions of behaviors, but we are pessimistic about the ability of any simulation method to represent directly the manifold adaptive pressures that emerge from even moderately complex ecosystems. Rather, we believe that adaptive pressures can be best understood indirectly, by setting up environments, simulating an evolutionary process to produce psychological and behavioral adaptations to those environments, and comparing the resulting adaptations and behaviors to those observed in real organisms. Dynamic programming represents an attempt to understand the results of evolution without simulating evolution. But we believe that evolution can take care of its own. Simulating evolution via genetic algorithms can automatically register the differential selection of genes and gene complexes through the phenomenon Holland (1975) calls *intrinsic parallelism*, and can include the effects of kin selection and inclusive fitness.

Furthermore, through the application of our genetic algorithm to the evolution of behavioral-producing neural networks our models of adaptive psychological mechanisms can incorporate the two main advantages of the dynamic programming approach: first, the use of *evolved*, not prespecified, internal state variables in the generation of behavior (via recurrent patterns of network activation – see Elman 1988), and second, the production of ongoing dynamic behavioral sequences (Jordan 1986). Moreover, our method includes the further biologically relevant characteristics of a powerful set of learning mechanisms (Rumelhart & McClelland 1986) and the ability of networks to generalize adaptively to novel environmental situations (a crucial adaptive capability – see Shepard 1987), obviating the need for an exhaustive dynamic programming search of state-space.

If you want to model what comes out of the process of evolution (behavioral adaptations) in terms of what goes in (adaptive pressures) then why not model the process itself? The growing number of researchers using genetic algorithms answer "why not, indeed?" Genetic algorithms are transparently analogous to natural selection, applying concrete environmental and social effects to genotypically coded populations of organisms which evolve forward in time, thus performing computationally efficient searches for adaptive responses to emergent adaptive pressures. As such, they are an intuitively appealing, understandable, and tractable approach to modeling behavioral adaptations. Respect for the complexity of natural behavior demands respect for the adaptive process, natural selection, which produced that complexity. And instantiating that process in our models is the highest respect we can offer.

The “crooked bookie” cycle

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Dynamic programming is one of the more promising new approaches to the modelling of behavior and life histories. Clark's advocacy is clear, simple, and compelling. The strong points of his model – for example, the intertemporal trade-offs, the single currency, and the technique of backwards induction – are well advertised without the dodging of difficulties. I found Clark's careful treatment of the criticisms and misgivings expressed by commentators on the earlier Houston & McNamara (1988a) piece particularly helpful. My only reservation is that perhaps Clark would do better to turn the “excessive generality” of his approach from an apparent vice into a proclaimed virtue. At the moment, the application of the model to any particular behavioral subproblem, fledgling for instance, is apt to recall butterflies being broken on wheels. Too much theory and too much computer power is needed to cope with rather modest problems. The best defence against this criticism is surely to stress the generality of the model rather than to apologise for it.

One issue I would have liked to see taken further is the involvement of local environmental states in the behavioral decisions of organisms and the reciprocal involvement of the behavior of organisms in local environmental states. I think this two-way linkage between organisms and their environments, which Clark acknowledges in both Figure 1 and section 2, is an intimate one, and it may be more important than Clark's tentative treatment of its implies.

The major point is that the current state of an organism's local environment, which it “observes” before it “decides” its next act $A(t)$, may itself have been previously changed by a previous act from that same organism (or possibly a genetic relative or a reciprocal altruistic partner). There is therefore a cycle connecting organism states to local environmental states via organism acts. One effect of this cycle is its influence on the informational states of organisms (subsumed by $X(t)$). For example, if an organism selects or perturbs its own habitat by moving somewhere else, or by consuming a resource, or by dumping detritus, it is bound to induce some change in the state of its own local environment (or the environment of other organisms, including its own offspring). In this case, the next time around, when the organism “observes” the state of its local environment again, the information it now receives from its environment will be different as a result of its own prior acts. Different information gained from a changed environment, however, will promote different “expectations,” different decisions, and different behavioral acts.

The logic here is intriguing, and has been partly explored by John Campbell (1985) in terms of what he calls “future self reference,” or more simply, the “corrupt bookie” problem. As Campbell says: “A future self-referent system that also has the mechanical ability to operate on the physical world around it, is capable of extraordinary causal behavior” (p. 162). For example, it can set up self fulfilling prophecies. Thus, a “corrupt bookie” not only predicts which horse is going to win the race, but he also fixes the race to ensure that his prediction turns out to be correct. The opposite can also happen. The bookie may fix the race first, and only then realise, via a change in his informational state, that he's now set himself a new problem. He now has to change his predictions and his next behavioral act if he wants to stay in business.

In principle, the same logic works at the population level too, where it is likely to affect the life histories of populations and the rates and directions of their evolution. One relevant suggestion from Wilson (1985) and his colleagues (e.g., Wyles et al. 1983) is that rates of evolution may be affected by a “behavioral drive” (one that corresponds quite closely to the feedback arrow from

$A(t)$ to $Y(t)$ in Clark's Figure 1). Both Wyles et al. and Wilson treat behavioral drive primarily as an evolutionary accelerator. It could equally well serve as a brake, however, because organisms can behave “conservatively” as well as “opportunistically.” For example, a conservative strategy might involve a population of organisms consistently selecting for habitats for which the organisms' genetically based adaptations were already suitable, and consistently withdrawing from or avoiding other habitats for which they were genetically unsuited. This “future self reference” logic is only partly captured by conventional models of intraspecific competition in population genetics, for example, by those models concerned with habitat selection or frequency dependent or density dependent selection (Hartl & Clark 1989), or by other related ideas in evolutionary theory such as Dawkins's (1982) extended phenotype. There is still plenty of scope for improvement. Clark's dynamic programming might help.

One possible way forward might be to let the $X(t)$ variable subsume not only the organism's morphological, physiological, and psychological states at time (t), but also the states of those components of its local environment for which the organism itself (or, at the population level, its genetic relatives) was responsible via its own prior niche perturbing and niche selecting acts. The rationale here is that the self-induced components of any organism's local environment should be derivable by “backwards induction” from the organism's terminal fitness function $\Phi(X(T))$, because the changes caused by goal-seeking organisms in their local environments are typically not random; they are directed by $\Phi(X(T))$.

The effect of this adjustment would be to shift the boundary between the $X(t)$ and $Y(t)$ variables to the point where $X(t)$ subsumes not only the organism's assessment of its own local environment, but also the physical location and the physical state of its environment insofar as the organism itself is responsible for determining that location, and for causing that physical state. The $Y(t)$ variable would then represent all the remaining components of the organism's environment for which the organism itself was not responsible, but which instead originated from genuinely independent events in the rest of the environment.

Elsewhere (Odling-Smee 1988) I've described this stretched version of the $X(t)$ variable in terms of an organism-environment interactive relationship called the (OE). I've also suggested that, contrary to common sense, a succession of (OE) states might be a better basis for understanding the activities and life histories of organisms, than a mere succession of organism states. The potential advantage of this idea is that the (OE) variable (= the stretched $X(t)$ variable just described) can cope with the “crooked bookie's” future self referent cycle, whereas the present $X(t)$ variable cannot. In practice it may be harder to measure successive (OE) states than successive organism states, but probably not much harder. All contemporary measures of organism states are already quasirelativistic (i.e., the concept of a niche is already relativistic, even though the concept of a habitat is not), and as such they refer implicitly to the states of organisms' local environments as well as to the states of organisms. By contrast, measuring organism states *in vacuo* makes no biological sense at all.

Regardless of what Clark thinks of this idea, I welcome his model. I hope it proves possible to develop it. I think it will.

State variable models are powerful, not perfect

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The fact that Clark lists me as someone who seriously faulted the state variable approach of Houston & McNamara (1988a) indicates that my commentary was not clear. I have long agreed (Partridge 1976) with Clark that the state variable method of modeling and its reverse in Bellman's (1961) optimization method are powerful, perhaps even necessary, tools for understanding complex biological function. Avoiding the slipperiness of verbal models, these models can deal with the multidimensional, nonlinear, and dynamic systems that living systems are; most other models cannot. The state variable approach is a great but imperfect tool; its acceptance will grow if its limitations are well respected.

State sensitivity. Some systems are so sensitive to initial conditions that starting from indistinguishable but different conditions, two identical systems will soon develop widely divergent states (Devaney 1989; Holden 1986). A state variable model of such systems will also reveal this unpredictability. On the other hand, if a real system converges on an "optimal" state, a model of this system in reverse time will diverge unpredictably. Likewise, the necessity of discrete time representation in the models for digital computation introduces complex and often misleading deviations from the ideal trajectory of the modeled function. Thus, a real system may behave well, whereas its model does not give stable results.

Model selection. Beyond these technical problems lies the question of what is optimal. In an entertaining short videotape, Ackley and Littman (1990) show a state variable model of evolution of simple learning. Although many "species" died out, "Adam's descendants" evolved a "good enough" solution (Partridge 1982) that was better than a handcrafted "perfect" solution because the imperfect solution had less impact on the environment, an issue overlooked in the "perfect" case. Although these investigators recognized the omission of a critical point, we are not all as alert to our own oversights. When using state variable models, we should heed what Pavlov has been quoted as saying: "I do not judge students by how much they know but by how much they question their ideas." It is too easy to believe our own models.

A mathematically sound optimization method gives us no guarantee that we have chosen the problem that was discovered by the evolution of that better solution we study. The trail of evolution is marked by a series of bifurcations beyond which further optimization may go in different directions. Thus, we are unlikely to expect a primitive turtle to benefit as much by developing escape speed as by developing a tighter shell closure. Yet optimization for a thin-skinned salamander might lead to long, thin leg bones. All dichotomies in optimization criteria may not be so obvious, but can be just as critical to meaningful modeling.

Beyond reproduction. One criterion for evolutionary selection that is easy to accept is survival to reproduce and the accomplishment of reproduction. Evolution is sometimes claimed to make no contribution to function after reproduction. Is this valid? Does not the primate colony with related genetics have some advantage if the postfertile and well informed females relate to and teach the young males? One might suspect that the educational advantage of cross-age association may have had a role in the primitive development of sexual pairing even in humans. At the moment, I am impressed by the possibility that evolution may even contribute to traits after the death of the individual. The hardened thorns of dead blackberry bushes seem to provide an effective protection to maturing first year bushes, yet they still allow seed dispersion from mature plants

by birds. That patch of closely related plants seems to have an advantage in surviving to disperse its fruit if the dead canes have large hardened thorns.

A powerful modeling tool need be no threat to any of the good field biologists who are needed to keep our models realistic. A lack of either insight or skepticism should eliminate modelers as well as describers. On the other hand, as simple questions are answered, the more complex remainder becomes too involved for unaided intuition to be a reliable guide.

Model limits. In this time of first and even second generation models, we study major effects and tend to extrapolate from the current effectiveness of state variable models to more complete models. We recognize the "curse of dimensionality" but hope the continuing growth of computer speeds and storage can push back the limits this imposes. There may still be a theoretical limit on the optimization process in state variable models. Today, modeled variables deliver effects much larger than the residual differences between the model and the real system. Later, as we study more detail, the contribution of individual features can be small and perhaps much smaller than the still unidentified residua. In addition, small deviations in major factors may obscure the total effect of the small detail, especially if the factors are not independent of each other. Is it possible that in more detailed models isolating the individual effects of secondary factors will become as difficult as separating summed exponential decays?

Keep on modeling. I will look forward to seeing more state variable models and their optimization in behavioral evolution, but would warn potential authors that, at least in the bio-engineering journals, referees are no longer impressed by good math alone; they also expect it to be accompanied by sound intuitive self-criticism. Still, it is hard to believe that observation and intuition can carry understanding much deeper into complex biology without the aid of formal tests of the internal consistency of ideas such as the use of state variable models and optimization.

Rule of thumb

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Clark has offered a thoughtful and unpretentious account of how dynamic optimization theory can be applied in behavioral ecology. It seems obvious that this approach is needed, and, from my perspective, it is difficult to understand what all the fuss is about. In the simplest form of optimization problems, one simply solves for a number, such as the optimal distance for chasing prey of a given size. In many circumstances, however, the optimal behavior of interest cannot be represented by a single number; it must be represented by a function of time. That is, the optimal behavior changes as the animal grows and ages. Dynamic optimization theory is simply a mathematical tool to predict an optimal function, instead of an optimal point. As Clark has mentioned, dynamic optimization theory has developed from the classic calculus of variations. The method Clark describes, using the so-called Bellman equation, is one technique. Another, involving the so-called Pontryagin maximum principle, has also been popular.

Whether an organism actually conducts a sophisticated calculation to determine what behavior is optimal for it is not a serious question. Obviously, when a flycatcher grabs a moth from the air, it has not explicitly integrated Newton's equations of motion. Yet, somehow its behavior amounts to the same thing. There is a need to explore how simple behavioral decision rules ("rules of thumb") predict behavior that converges on an optimal solution that we mere humans can only deduce with an

expensive computer. This need for understanding how zoologically plausible rules of thumb work is logically independent of the techniques needed to compute what an optimal solution is. Clark's target article, and the book by Mangel & Clark (1988), help to make these relatively new mathematical techniques more readily accessible, and offer some stimulating examples.

Short-term behavior and long-term consequences

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Because natural phenomena are for the most part rather complex, models of the real world are formulated to extract only the aspects under scrutiny and to compare the properties so derived with empirical observation. Given the extensive discussion in the literature on the validity of modelling, and in particular of models that describe the value of behavior for the survival and reproduction of the organism (e.g., Pierce & Ollason 1987; Stearns & Schmid-Hempel 1987), one can only hope that by now the proper role of "optimization" is understood in all quarters. It is accordingly time to concentrate on the more immediate problems and promises of such powerful modeling techniques presented in Clark's target article.

Behavior is a process that unfolds over time and its effects are actually to change, restore or maintain an individual's state (McFarland & Sibly 1972). This temporal dimension is not always welcome, however. For many questions in animal behavior, great care is taken to balance time effects by experimental designs to expose the one process of interest, for example, controlling for time of food deprivation when studying the relative intensity of response to a food stimulus. Such questions arise more often when one is studying the mechanics of behavior, whereas the question of how behavior affects fitness naturally puts more emphasis on change over time and eventual outcome. It is in the latter domain that dynamic programming models are obviously more useful.

This having been said, it would be too much to expect that dynamic models can resolve some of the intrinsic difficulties and weaknesses of modeling, for they only add the dynamic components without basically altering the logic of static models. Models are still evaluated through their power to explain observed phenomena; assumptions about constraints, strategy sets and implemented goal functions are thereby tested. Contrary to Clark's contention, I think that static models have done quite well in this respect. For example, the assumption of random encounters with prey items was found to be incorrect and the models were amended accordingly (Rechten et al. 1983); similarly, different fitness tokens could be critically compared in nectar-collecting honeybees (Schmid-Hempel et al. 1985), thus providing some insight into either perceptual constraints or long-term consequences. Furthermore, as in the case of static models, assumptions about constraints and implemented goal functions in dynamic models are likewise interdependent. Clark's (and Houston & McNamara's 1988b) presentation emphasizes terminal reward function as a fitness token. The problem could also be formulated in terms of an intermediate function, however, one that is constantly updated in the course of the process instead of just after a terminal reward (Intriligator 1971). Terminal rewards are of course more appealing in many biological contexts, such as the small-bird-in-winter paradigm where body weight at the end of the day is a reasonable indicator of future survival probability.

Clark also discusses qualitative testing of dynamic models. Indeed, there are cases where the qualitative predictions are

interesting, for example, the prediction that plants (e.g., with linearized dynamic equations) should allocate resources into growth versus reproduction in an all or nothing manner (the bang-bang policy). Although such a strict bang-bang pattern is hardly ever observed, the insight provided by this analysis is helpful. On the other hand, qualitative predictions are often in danger of being rather trivial. In Ydenberg's (1989) example, chicks face a trade-off between growing safely but slowly in the nest versus growing fast but at higher risk out at sea. It is therefore to be expected that some intermediate best fledging time exists if the terminal weight of the young is to be maximized. Apart from the fact that this scenario alone hardly warrants a dynamic model (as opposed to a static one), this prediction alone is not very surprising. The story is different, however, if quantitative predictions are derived (as in Ydenberg's case). Quantitative predictions are never trivial, since there is no a priori way to see why fledging time should be 35 rather than 27 days. Dynamic programming by numerical computation is not terribly well suited for qualitative predictions, as usually only a limited domain in parameter space can be analyzed.

Despite such shortcomings, I feel that the formulation of the dynamic problem in terms of maximizing (or minimizing) a terminal reward function offers some intriguing perspectives. In particular, it naturally lends itself to analyzing the relationship between a minute-to-minute behavior and the longer term consequences following from adopting a particular behavior. It is this link of which we know almost nothing. Yet this connection is crucial if we want to understand how variation in instantaneous behaviors, motivational states, risk assessment, and so forth are related to selective forces that are thought to be responsible for the evolution or eventual maintenance of these traits. In life history theory this relationship is at the very heart of the problem. Dynamic solutions have thus been used in this area for some time (e.g., Schaffer 1983). In fact, Equation 10 is basically analogous to Fisher's reproductive value, although the latter concentrates more explicitly on age-dependent fecundity versus survival schedules of competing genotypes in a population.

Static models have been used with success both in life history theory (e.g., Stearns & Crandall 1984) and behavioral ecology (Stephens & Krebs 1986). Given the importance of change in an individual's state and available opportunities, one is left wondering why such models have done so well. Actually, as Clark points out, dynamic models show such an interesting convergence property that the best strategy becomes independent of time when terminal time is still a long way ahead (or, if negative, exponentially distributed). Moreover, it is often found that the best strategy may be insensitive to current state under a broad range of conditions (e.g., foragers should almost always generalize their diet choice with long travel times between depleting patches: Lucas & Schmid-Hempel 1988). Although this does not necessarily imply that the situation becomes static, static models may become a reasonable approximation over large regions in state and time space. As the same decisions would have to be made under many conditions, it seems reasonable to expect that this selects for simple decision rules. It would therefore be interesting to learn more about the proportion of an animal's life that is within such "quasistatic" domains and hence perhaps to deduce the relative selection pressures on simple versus complex decision rules, or to understand in which way the overall complexity of state and time faced by the organism could be broken down to simpler compartments.

It is not always clear, however, what a simple rule is: Suppose that a best strategy requires a foraging animal to move along a straight line through a food patch. Although this seems like a very simple rule, it may be difficult to achieve in living beings. In fact, most animals meander while moving along, which reflects the constraints and imperfections of the locomotory apparatus. Thus, contrary to the apparent simplicity of a

straight-path rule, rules that require tortuous paths may actually be much simpler to embody. A slightly disturbing message that dynamic models seem to convey, however, is that such (convergent) best strategies may often not depend on the precise formulation of the fitness (terminal) function. This is of course very helpful in some contexts, but it is uncomfortable for evaluating the predictive power of alternative formulations of "fitness." Because there is no universal definition of fitness, one use of models is to help to identify the most likely candidate.

Finally, Clark makes a number of recommendations about when to use dynamic models. Some of his suggestions may give a wrong impression of the logic of static models. For example, the traditional models of optimal foraging also differ in the same way as dynamic ones do from models that imply utility or indifference contours to study behavior. In fact, what distinguishes them is not the dynamic versus static dimension, but that a strategy is derived from a normative prescription based on a priori reasoning about how natural selection acts rather than in a descriptive way, that is, by observing the animal's indifference to combinations of factors (Krebs & McCleery 1984). Similarly, testability, quantitative predictions, and trade-offs too are essential ingredients of static models. Plainly, dynamic models are appropriate when the dynamic changes over time actually become important. This should most often be of interest when one wants to link the short-term behavioral strategies, as investigated by ethologists and behavioral ecologists, to life history considerations, the domain of population biologists and ecologists. Still, behavior can be analyzed from many different and quite heterogeneous points of view that neither can nor should be unified. Hence, it is basically with respect to the integration of different time scales that dynamic programming models can contribute most toward a much needed step of unification in biological thought.

period at the end of winter. Each day is divided into 200 time units. An unpaired bird normally has three behavioural options: foraging alone, foraging in a flock, or singing to attract a mate. The number of possible behavioural sequences for an unpaired bird over the five day period is $3^5 \times 200 = 10477$. The most efficient way (perhaps the only way) to find the optimal policy in this case is by backward dynamic programming.

For a model involving a single behavioural decision, however, such as Ydenberg's model, simple optimization promotes a greater understanding of the results. Fledging mass, mass at the end of the season and the overall fitness of the chick can easily be obtained for suboptimal as well as optimal policies. The position of the optimum can be better understood by observing how the components change in relation to each other as the optimum is approached.

Another drawback to dynamic programming is that it is harder to check than a simple analytical or numerical solution. We have tried to duplicate Ydenberg's dynamic programming method but have been unable to produce the same results. When a dynamic programming model is presented, the computational methods used should be described; the interpolation technique is one item that Ydenberg does not describe.

Finally, there is the need for sensitivity analysis. One should be wary of sweeping generalizations concerning the sensitivity of dynamic programming models or other mathematical models in biology. We have found that the predictions of Ydenberg's model are insensitive to some parameters which would be considered biologically important (such as mass at hatching) but highly sensitive to the arbitrarily chosen form of the terminal survival function: a nonlinear function ($1 - e^{-0.01(x-700)}$) gives an optimal fledging time of more than 20 days later than the linear function. On the basis of these results, we feel that the predictions of this model should be treated with caution.

A not so backward way of thinking

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Clark's example of a dynamic programming application (Ydenberg 1989) is unfortunate. This work has been examined in detail (Byrd et al. in press): the main observation is that the Ydenberg model is a straightforward optimization problem for which dynamic programming is not needed.

The probability of a chick surviving from hatching to the beginning of the breeding season is the product of four terms: (i) the probability of avoiding predation whilst in the nest (i.e., before fledging), (ii) the probability of surviving the journey from the nest to the ocean, (iii) the probability of avoiding predation whilst in the ocean (i.e., after fledging) and (iv) a mass dependent "terminal survival" function for the probability of surviving from the end of the period modelled (the first 90 days of the chick's life) to the beginning of the next breeding season.

In Ydenberg's model, (ii) is constant; (i) and (iii) can easily be calculated as a function of the fledging day, as can (iv) as growth is deterministic. Hence one can calculate a chick's overall survival probability as a function of the day on which it fedges. Then by running through all possible values of fledging day (from 1 to 90), the day which maximizes overall survival probability can be found. This is the optimal day for fledging.

Dynamic programming is not required because the Ydenberg model involves the chick making a *single* behavioural decision: when to fledge. Where dynamic programming is useful is in the study of a *sequence* of decisions. Szekely et al. (in press) provide a more appropriate example of dynamic programming: The behaviour of a small passerine bird is modelled over a five day

Pitfalls and promises of behavioral modeling

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Clark has provided us with a spirited defense of optimality models in general, and dynamic programming models in particular. In the main, his points are well taken, although occasionally his enthusiasm for the topic leads to an over sanguine view of dynamic programming's potential for solving the world's ills. For example, nonlinear relationships are common in nature, but they may be difficult to integrate into dynamic programming models. In addition, these models are often so complex as to discourage workers from the recommended, but necessary course of examining and testing each component for biological verisimilitude (sect. 6, Excessive generality).

Indeed, although Clark correctly emphasizes the need to examine carefully and to validate the assumptions underlying any type of theoretical model, this step is absent even in some of his own recent work. There seems to be an unfortunate tendency for empiricists and theoreticians alike to consider some assumptions so basic as not to require testing, with unfortunate results (e.g., Davies 1989; Stamps, in press). Dynamic programmers often share the tendency to "inherit" basic assumptions from previous papers in the empirical or theoretical literature, and then to incorporate them into their own models.

A case in point is the series of models on optimal group sizes in lions. Initially, workers assumed that lions associated in groups in order to optimize foraging success (e.g., Caraco & Wolf 1975; Schaller 1972). These early models, however, generally predicted group sizes smaller than observed in nature. Subsequent modelers did not stop to reexamine the basic assumption that group sizes were driven by foraging considerations, but instead

added new parameters, greater complexity, more realistic biological processes, and fancier analytical techniques, including dynamic programming (e.g., Mangel & Clark 1988; review in Packer et al. 1990). These complex models, however, continued to predict group sizes different from those in which lions are actually found. Rather late in the game, field workers began to reconsider the premise that lion groups are "for" foraging. For example, Packer et al. (in press) have argued cogently and persuasively that relatively large group sizes in lions may be required for effective territory defense.

The hypothesis that group sizes are relevant to defense in group-territorial animals is hardly new (e.g., Brown 1982). Yet modelers have for 15 years clung tightly to their original assumption that lion groups are related to foraging, even in the face of predictions that did not fit the observations, and even though alternate, biologically reasonable assumptions were available and ready to be incorporated into new models. Clark seems to think that future modelers can be convinced to validate all of their assumptions and to create new models if there are discrepancies between observations and predictions; given past history, I am not so sure.

Curiously, Clark seems to have neglected one of the more promising applications of dynamic programming in behavioral ecology. He notes that animals may not optimize, and that they particularly do not optimize using the complex equations and mathematical gymnastics typical of dynamic programming. Conversely, he emphasizes that it may be useful to know what the optimal behavior *would* be, assuming that all of the assumptions and parameters in one's model were correct (sect. 6, Simple decision rules, para. 2). Unfortunately, this leaves a lot of middle ground between the "ideal" behavioral strategy predicted by a particular model and the intuitive feeling of many empiricists that animals would be hard-pressed to achieve optimal behavioral strategies to handle all of their problems.

Dynamic programming can also be used in another way, however, to identify "zones of indifference" around an optimal behavior. In some situations, any of an array of alternative behaviors may yield payoffs nearly as high as those produced by an optimal behavior. For example, we can envision a hypothetical situation in which one individual makes a perfectly optimal series of decisions and achieves a fitness equal to X, whereas other individuals make errors of one sort or another, but achieve fitness values ranging from .95 to .99X. In other words, while there may be only one optimal behavioral strategy in a given situation, there may be a large number of only slightly suboptimal strategies. Given the lack of precision of even the best theoretical models (sect. 2, para. 3), and given the many reasons why animals may be unable to evolve perfect adaptations to solve particular problems (e.g., Arnold 1987; Kirpatrick & Lande 1989; Maynard-Smith et al. 1985), it may be unreasonable to expect an exact fit between a predicted optimal behavioral strategy and actual behavior. On the other hand, if the optimal behavior is surrounded by a large zone of indifference, it wouldn't be unreasonable to expect real behavior to map somewhere within this zone. In particular, rules of thumb may work because they produce results not terribly different from those expected of an optimal behavior (e.g., Janetschek & Cole 1981; Real, in press).

Ordinarily, the mapping of a behavioral zone of indifference is a tedious process, requiring the identification and computation of a fitness payoff not only for the optimal behavior, but also for each of a wide range of possible alternate behaviors. Dynamic programming can handle this task with relative ease, however; recent examples include studies by Roitberg (1990) on host selection by fruit flies, Mangel (in press) on patch selection by foraging animals, and Bouskila & Blumstein (submitted) on strategies for assessing predation risk. These studies yield similar results, namely, a wide range of possible behaviors that yield payoffs nearly as high as that produced by the "optimal" behavior. If these studies are any indication, dynamic programming

may prove very useful for bridging the gap between what animals actually do and what optimality models predict that they should do.

Variational principles, behavioural adaptations and selection hierarchies

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As Clark aptly remarks, dynamic programming has its roots in the calculus of variations, a celebrated mathematical method in theoretical physics since its development. For example, a stone thrown upward and falling free follows a trajectory that minimizes the variational effect of the time integral of kinetic minus potential energy. Somewhat surprisingly, the local equation of motion (Newton's second law) can be deduced from such a global rule (Feynman et al. 1964). [See also Schoemaker: "The Quest for Optimality: A Positive Heuristic of Science?" *BBS* 14(2) 1991.]

Variational principles and related approaches seem to percolate into biology. Although the equations of motion behind the variational principles in morphogenetic studies (cf. Goodwin & Trainor 1980; Molnár & Verhás 1990) are far from clear, dynamic programming provides us with (often simple) decision rules. As the decision rules are processed in animal brains, they can be regarded as local rules for behaviour emerging from brain dynamics. But how can such rules emerge and be stabilized?

In physics, quantum mechanical interactions using the associated wave-likeness of particles ensure that a particle "gets" some information about all possible paths from which the extremal one is finally chosen (Feynman et al. 1964). In biology, the loosely analogous choice of optimal behavioural rules is made through selection. Genetic evolution always underlies this process, but in the case of learnt rather than innate behaviour Darwinian selection within the brain itself may be important. Let me explain.

First assume that the behavioural trait in question is innate. Although evolution in dynamic games has not yet been modelled, analogous developments in "static" game theory do exist. If we model the selection process for different strategies, it turns out that ESSs (evolutionarily stable strategies) must be asymptotically stable rest points of the associated equations (Maynard Smith 1982; Taylor & Jonker 1978). According to the distinction of Vincent & Brown (1984), there is an inner game and an outer game; the former refers to the resolution of behavioural encounters, whereas the latter refers to the evolution of such resolutions. Conforming to this terminology, the outer games for dynamic games have not been modelled so far. (*Caveat*: there is a disturbing ambiguity of terminology involved here; the selection equations of the outer games of static inner games are often referred to as game dynamics, because they can be put into the general framework of dynamical systems (Hofbauer & Sigmund 1988), but this usage is not to be confused with that of dynamic programming). During natural selection, several different strategies are sampled, but only those with the highest relative fitness are kept. Evolution through natural selection can thus lead to optimal life histories *sensu stricto* (cf. Schaffer 1974) as well as *sensu lato* (Mangel & Clark 1986).

Now let us assume that the ESS of a dynamic game must be learnt. Interestingly, it has been shown for static games that, under certain restrictions, a learning rule that takes a population to an ESS is an ESS learning rule among the possible learning rules (Harley 1981). How would such a learning rule look for a dynamic game? In Harley's (1981) example, could the fact that recent payoffs should have a stronger effect on behaviour than earlier ones indicate some connection with the procedure of

backwards induction? ESS learning rules for dynamic games await elaboration.

Learned dynamic ESSs take us to the problem of optimality in the following way. Although we still lack a satisfactory model of the working brain (cf. Anderson & Palca 1988), a promising approach is neuronal Darwinism (Dehaene et al. 1987; Edelman 1987). According to these models, a kind of natural selection is going on in the brain itself, among neuronal groups. Selection of functional repertoires from primary ones is taking place in a manner compatible with the survival needs of the organism as a whole. As Michod (1989) emphasizes, a selection hierarchy is involved: Genetic evolution should lead to innate rules of the brain that ensure that most of the time adaptive behavioural patterns are allowed to emerge through neuronal Darwinism. As in the analogous cases of hierarchical selection ranging from earliest evolutionary units (Szathmáry 1989) to recent genetic ones (Dawkins 1982), the higher level system must be able to constrain the evolution successfully at the lower level; otherwise the higher unit is disrupted. Whereas selfish genes (including those affecting behaviour) have received wide attention, selfish neuronal groups leading to nongenetic and organismically maladaptive behaviour remain largely unnoticed. Inasmuch as these are of importance in the behaviour of (presumably) the most intelligent animals, deviations from optimal strategies as implied by the dynamic programming approach are to be expected. Although it is relatively easy to calculate the frequency of selfish genetic elements in spread-selection balance (Charlesworth & Charlesworth 1983), analogous calculations will, I fear, be very difficult to make in the case of behaviour.

Finally, it should be realized that selection hierarchies imply the simultaneous application of different time scales (Szathmáry 1989). A dynamic inner game and the outer game describing its evolution proceed at two time scales: characteristic times for the former are shorter than the organisms' generation time, whereas those for the latter are markedly longer. Learning through brain dynamics introduces yet another time scale.

Modeling change in biology and psychology

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As Heraclitus observed about 25 centuries ago, all things change in nature (i.e., change is the highest form of invariance). Whether change should be the emphasis of natural theory depends on the speed of alteration relative to the events and structure under study. Clark makes a strong case for dynamics in the instance of behavioral adaptation. Because I am a psychologist, I will parallel remarks that are specific to the present topic with comments on dynamics in psychology. It seems to me that many of the concerns and problems are the same in psychology and biology.

William James observed that consciousness is like a stream, ever changing and continuous. Many great psychologists have neglected that notion. Dynamics have primarily been seen in learning theory (now again on the ascent, particularly in connectionism) and certain sensory and information processing oriented approaches. By and large, however, most areas of psychology (including cognitive, clinical, psychobiological, and developmental) have tended to view their phenomena as separate states with little concern for how one gets from one state to the other. Formal decision theory was an example of this neglect of change and process, with an overemphasis on static utilities and subjective probabilities. (Recently Jerome Busemeyer and I have been attempting to develop a more dynamic yet still quantitative theory of decision making: Busemeyer 1982; Townsend & Busemeyer 1989). (Because of the ubiquity of

change and process in psychology and biology, I would go so far as to suggest a course in dynamic systems theory and process modeling for all Ph.D. candidates in these disciplines).

There was some slight confusion in the target article between qualitative versus quantitative and dynamic versus static. These are not the same and it is important not to confuse them.

One parallel between behavioral adaptation and psychology is the use of optimal modeling. Optimal modeling can serve not only as a substantive theory as suggested by Clark, but also as a useful base point against which to compare real behavior (e.g., as in signal detection theory, cf. Green & Swets 1966). This may be even more important in natural biological settings, where laboratory research is often precluded, than in psychology, where many phenomena can be explored in laboratory settings.

Now for more specific comments and questions:

1. Even though *BBS* is not the place for a detailed theory presentation, it is important not to gloss over critical facets. Consider the claims about convergence and the independence of $A^*(x)$ in Section 6, paragraph 3. There are always important conditions on which convergence depends. In what sense is $A^*(x)$ independent of the terminal fitness function? The reader may imagine circumstances where it should not be, or where the theory would be trivial if it were.

2. On the capturing of the past through the present state: There may exist systems where the present state is not sufficient to specify the conditional probability distribution on the next state. In this case, one may expand the notation to include past states and their even their associated times, thus generating a higher order Markov process.

3. I agree with the remarks about too much complexity vis-à-vis the amount of, and information in, the data. For instance, causal modeling in psychology and in other behavioral science areas suffers from a combination of sophisticated models with a paucity of data. This can also be a problem with an over-reliance on multidimensional scaling in the absence of substantive theory. The result is an unfortunate lag in scientific progress using those procedures.

4. The matching phenomenon may be a good example of a different variety of optimality, but then it is incumbent on the dynamic theorists to develop a new model in which matching is optimal (does the cited work by Stephens (1987) accomplish this goal?).

5. The argument concerning the size of the advantage of optimal versus nonoptimal behavior is a slippery one. Unless there is a solid theory/methodology of measurement bridging data and theory, such reasoning can and will often be used for theory rescue rather than theory testing.

6. Finally, the particular avenue taken by Clark and his colleagues appears to be more *immediately* fruitful than those placing too much emphasis on the modish but risky chaotic-dynamic approach (see, e.g., Townsend, in press).

Using models of behavior in optimal fashion

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1. **Introduction.** Clark argues persuasively for the usefulness of the dynamic approach to the modeling of behaviors. Dynamic models represent a more sophisticated mathematical treatment of behavior but the level of sophistication of a model is not necessarily the criterion by which its usefulness should be judged. The usefulness of this class of models for understanding patterns of animal behavior arises from two attributes. First, dynamic models can be used to examine situations that cannot be adequately addressed by static models. Second, for many

problems dynamic models are more reflective of what evolution through natural selection is likely to have wrought than static models. The philosophical difficulties that many workers appear to have with dynamic models arise with static models as well. In this commentary I discuss first the usefulness of dynamic models and then the problems that arise in the testing of any model that investigates an "optimal" behavior.

2. The applications of dynamic models. Many behavioral patterns cannot be addressed adequately by static optimization models. The model of fledging behavior presented by Clark epitomizes a variety of behavioral problems in which the "decision" at any time is a function of two or more dynamic state variables that may themselves be interrelated. Other examples include ontogenetic habitat shifts (Werner & Gilliam 1984) and feeding rates and habitat use as a function of reward levels and predation risk (Gilliam & Fraser 1987). There are a host of nonbehavioral problems that are completely analogous such as the timing of amphibian metamorphosis (Alford & Harris 1988) or the apportionment of physiological reproductive effort among clutches as a function of female age, reproductive history, and environment (Travis et al. 1987). Static models simply do not adequately capture the nature of the problem that the animal must solve.

Dynamic models, especially those of behavior, are more accurate reflections of what natural selection is likely to have produced, that is, not so much an optimal behavior but an optimal pattern of response to a set of changing environmental conditions. Evolutionary biologists have been turning their attention away from a search for a single adaptive trait to a search for an adaptive pattern of phenotypic expression in response to environmental cues. This change in outlook is reflected in models that examine patterns of phenotypic flexibility (Stearns & Koella 1986) and in experimental investigations of how patterns of variable trait expression may reflect adaptations to variable environments (Trexler et al. 1990). Behavior has long been thought of as the most flexible of traits and the use of dynamic models of behavior represents an evolutionary realism that is on a par with advances in modeling other phenomena.

3. The use of optimization models in general. Clark cites many of the papers that debate the use of either static or dynamic optimization models. The criticisms of optimization models rest primarily on two points, that evolution may not produce optimal behavior (or optimal anything) and that the testing of optimization models represents an exercise in circular reasoning.

It will always be hard to demonstrate that evolution has produced the optimal level of any variable. In a varying real world the mean phenotype in any given generation will often not match the optimum phenotype for that generation because of the lag time in the evolutionary process (Taylor in press). This result does not mean that selection does not work toward an optimum, only the genetic constraints hinder the realization of the optimum. The simultaneous study of genetics of phenotypic variants can help diagnose such a situation. A number of demonstrations of optimizing selection among phenotypes might not withstand close critical scrutiny (Travis 1989). Nonetheless, there is ample evidence that in many cases evolution has optimized *something* (Travis 1989); the question is whether what has been optimized is the value of a particular trait or the functioning of the whole organism. It would seem extreme to assert that evolution does not optimize; the conceptual problem is finding out just what has been optimized. It seems obvious that dynamic as well as static models of optimization can play a useful role in resolving this problem.

Citing circularity in the use of any sort of optimization model is an accurate criticism of the ways in which many such models have been used. This situation is unfortunate. Mathematical models are useful in two ways. First, they illustrate the logical consequences of certain assumptions or relationships among key variables, consequences that are ambiguous in verbal formulation (Iwasa & Teramoto 1980). Second, they serve as irreplac-

able guides as to which variables are critically influential and which are relatively unimportant in determining the quantitative range of the phenomenon one is investigating (Travis 1982). When used this way, optimization models can reveal the posited net behavior of the system and can guide the empirical investigator toward the most appropriate measurements. The "match" or "mismatch" of prediction and observation is not meaningful without thorough empirical investigations of the basic tenets of the model. Most of the exercises in circularity that have appeared in this context originate in the uncritical acceptance of functional forms of relationships among variables or unconfirmed assumptions about constraints. The modeling process and the models themselves cannot shoulder the blame for their nonoptimal use by empiricists.

ACKNOWLEDGMENT

My research is currently supported by the National Science Foundation, BSR 88-18001.

Testing predictions and gaining insights from dynamic state-variable models

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Not long ago the difficulty of analyzing the behavior of animals in many trade-off situations seemed daunting indeed. The main problem lay in expressing the costs and benefits of different behaviors – feeding versus hiding from a predator, or feeding versus territorial defense, for example – in the same way. The idea of "fitness units" provided a conceptual aid, but was of little value for practical measurement of experimentation in the field, though sometimes general predictions could be made and tested (see Martindale 1982). In 1982, it seemed that dynamic models offered the best hope for analyzing and understanding trade-offs, in spite of the awkwardness and restrictiveness of the techniques then available (Ydenberg 1982). Only a few years later, however, a simple and general dynamic modelling technique was developed that appeared to resolve many of the difficulties. This technique – stochastic state-variable dynamic programming – is detailed in the target article by Clark, and in an earlier target article by Houston & McNamara (1988). Though I was very familiar with the early works in behavioral dynamic programming by Katz (1974), Craig et al. (1979), and with the work of McFarland and his students (McFarland 1977), and had used dynamic programming myself (Ydenberg & Houston 1986), I became convinced of the power of this new technique in May 1986. During an afternoon meeting at Simon Fraser University, Alasdair Houston and Colin Clark jointly worked out, on a blackboard in front of a small audience and in a few minutes, a simple state-variable model for a problem a colleague and I had been interested in: calculating the fitness-maximizing life history of anadromous salmon species. I remember clearly how surprised we all were (including Houston & Clark) at the model's simplicity and elegance, and our pleasure with its depth and ability to give us insights into the problem.

With this brief background I would like to use some of my own experience with the technique to expand on Clark's claim (sect. 6, para. 12) that dynamic models are readily testable. I believe that a more precise assertion would be that state-variable dynamic models can readily be used to generate testable predictions of several sorts. One method is called "forward iteration" and is discussed briefly by both Clark (1990) and Houston & McNamara (1988). It involves using the decision rules provided by the dynamic model's solution to compute the frequency

distribution of the state variable that would be observed if animals in a population used those rules. Houston & McNamara (1987) have used this approach in their study of daily routines.

A second source of predictions comes from examining the model for changes in the predicted behavior over time. For example, in a study of red squirrels (*Tamiasciurus hudsonicus*) in the Yukon, Price (1989) found that some mothers gave their territories to one of their offspring. An analysis using dynamic programming showed that mothers in poor condition near the end of the short boreal summer should bequeath their territory. This is in fact what Price observed. The model also predicted that mothers in good bodily condition early in the summer should bequeath, while those in poor condition should not (i.e., the reverse). Mothers are generally unable to gain good body condition early (they are recovering from breeding), but the model suggested the experiment of food-supplementing some mothers to help improve their condition more rapidly. The prediction that these supplemented mothers should bequeath is a strong one that could not have been made without a dynamic model.

Another example is provided in Clark's Table 1. Here a dynamic model (Ydenberg 1989) of common murre (*Uria aalge*) fledging behavior predicts that nestlings hatched later should fledge lighter. The quantitative prediction fits the field data very well.

A third source of predictions of dynamic models comes from looking for changes in behavior when some of the model's parameters are changed. The murre fledging model predicts that slower-growing nestlings should fledge at an older age, and at a lighter weight. An experimental test that manipulated feeding rates in a related species, the rhinoceros auklet (*Cerorhinca monocerata*), confirms this prediction (Harfenist, personal communication).

More general predictions can also be derived. The fledging model and others like it (Ludwig & Rowe 1990) show that the "transition boundary" between successive life history phases should be negative (at the optimal transition, the state-variable is smaller later in the season) under some trade-offs, but positive under others. Seasonal declines in fledging weight are well-known in many seabird species, but positive metamorphosis boundaries are known in some marine fish (Chambers & Legget 1987). The prediction of the dynamic models is that the trade-offs between growth and mortality in the different habitats occupied by the successive life-stages in these groups is reversed. This suggests several lines of comparative research.

The predictions in each of the above examples are fundamentally dynamic, and could not have been made without some way to incorporate the time dimension into the models. The predictions are of several different types, some quantitative, and some qualitative. All are testable.

I can also cite a few difficulties from my own experience. Dynamic models are often complicated, and once encoded for computation it may be hard to understand why certain patterns are predicted. It often requires much work to trace just how a particular region in the output is arrived at, and why it changes shape when certain parameter values are altered. When a second investigator arrives at different answers for the same problem, it is often more than just a matter of checking the math. Recently, Byrd et al. (in press) arrived at somewhat different answers for the murre fledging model, as did Roff (personal communication). It took some checking to find that they were in fact right, and to locate my errors. More investigators are bound to experience this, and the differences may not always involve clearcut mistakes. Climate modellers will be familiar with these problems.

A second difficulty is that the data required for testing sometimes cannot possibly be obtained. There is some irony in the fact that the salmon model alluded to above is such a case. In spite of all the data available for these species, the type and detail of data we require for empirical testing of the model are

simply not available. Hence this is probably a good example of a first-generation model "best abandoned at this early stage" (sect. 7, para. 4). Yet we felt the model was exciting and valuable for the insight it gave us.

Author's Response

Dynamic optimization: Let's get on with the job

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I wrote the target article with the aim of showing that the use of dynamic optimization models in behavioral ecology should not be controversial. By and large, I think the commentaries support this claim. My sympathies are with those commentators (Barto, Focardi, Hitchcock & Sherry, Houston & McNamara, Mace & Sutherland, Milinski, Roughgarden, Travis, Ydenberg) who say, in effect: What's the problem? Dynamic optimization techniques have been well understood for more than 30 years (more than 200 years if one goes back to the calculus of variations), and they're obviously relevant in biology. Let's get on with the job of developing and testing dynamic optimization models. If you're going to use optimization theory, you may as well be aware of the most powerful techniques available. This doesn't mean that you have to eschew simpler models (Houston & McNamara, Schmid-Hempel, Travis) – the art of modeling consists of using the best model for the problem at hand, where "best" certainly implies the "simplest adequate" one. I was surprised how few commentators mentioned this basic point. Indeed, many insisted that further complications should always be included.

Several different techniques of dynamic optimization now exist (Roughgarden); Ydenberg's comment on the ease with which stochastic dynamic programming (SDP) models can be applied in behavioral ecology is most significant. My collaborator, Marc Mangel, and I, both familiar with most optimization techniques, have often been astounded by the simplicity and flexibility of the SDP approach. Table 2 in the target article gives some idea of its scope, and many more diverse applications are now in progress. (I do worry, along with Alley, Houston & McNamara, Milinski, and Partridge, that SDP models may become faddish and used to excess, but, as Travis says, you can't blame the modeling framework itself for that.)

1. Some routine extensions

Several commentators have suggested extensions of SDP models that seem to be straightforward. Partridge observes that in some cases postreproductive activities may increase parental fitness by enhancing the fitness of offspring. This can readily be modeled by including

additional state variables for offspring. One obvious prediction is that parents will be more risk averse if their own survival will enhance offspring fitness.

Fantino discusses delayed-reduction theory, according to which hungry pigeons prefer to reduce the delay to their next reward at the cost of also reducing average food intake. This is exactly what a dynamic state-variable model predicts (Mangel & Clark 1988, Chapter 2); the possibility of a quantitative functional analysis may be worth pursuing.

Townsend points out that higher-order Markov decision processes may sometimes be needed; as he notes, these can easily be transformed to first-order models (by increasing the dimension of the state space), at least for finite-order processes. (I doubt that **Dickinson's** concern about infinite-order processes needs to be taken seriously.)

Alley faults foraging modelers for assuming thoughtlessly that food intake always implies positive net benefits when in fact predation risk, competition, need for water, and other factors may negate these benefits. SDP models, as described in the target article, are in fact ideal for dealing with such tradeoffs as these; many examples occur in the references of Table 2. **Schmid-Hempel** is still worried about including intermediate rewards as well as terminal rewards, but the target article clearly states how intermediate rewards (i.e., repeated reproduction) are easily included in the models. Intermediate rewards other than actual reproduction are accounted for by including appropriate state variables. Schmid-Hempel admits that dynamic models are appropriate whenever dynamic changes in behavior (or in the environment) are important. I would add that they are also appropriate whenever an organism's state may influence its behavior, and whenever tradeoffs are important (since tradeoffs invariably involve temporal opportunity costs). The state-variable dynamic programming framework allows for the unified treatment of these and many other aspects of behavior, including for example, inventory-related behavior (food caching: **Hitchcock & Sherry**).

2. More substantial generalizations

The application of SDP models to behavior is still in its infancy; many new directions await development. **Howe et al.** and **Odling-Smeet** call for the inclusion of environmental variables and the effects of behavior on local environments. Nothing in principle prevents this from being done (as I point out in the target article) – it's again simply a matter of expanding the state space. The curse of dimensionality (also model identification) awaits those who would do so willy-nilly.

The important question of *mechanisms* is raised by **Barto, Colgan & Jamieson, Focardi, Roughgarden, and Miller & Todd**. Some of the more mindless exercises in optimization modeling have come up with so-called optimal behaviors that were patently unrealizable – Colgan & Jamieson quote an extreme example. Although dynamic models could certainly make the same mistake, it should be noted that they are quite capable of restricting actions to those that are known or thought to be realistic. The specification of the set of feasible acts or decisions is entirely up to the modeler.

It strikes me that this might well be a rewarding area for future research. A whole sequence of models (for a given behavioral phenomenon) could be developed, differing only in the set of feasible actions. Then the fitness consequences of simple versus complex decision rules (including “rules of thumb” – see **Roughgarden and Stamps**), and of different mechanisms, could be assessed. Cases in which fitness could apparently be substantially increased by more sophisticated behavioral patterns would raise the question of what may have hindered the evolution of such behavior.

This leads me to a common misuse of the term “optimal.” Statements to the effect that “so-and-so has shown that such-and-such an observed behavioral pattern is nonoptimal” are often encountered. By itself such a statement is nonsense. What has usually transpired is that someone has constructed a model predicting certain optimal behavior, and someone (not necessarily someone else) has observed that certain organisms regularly fail to behave as predicted. All this proves is that the observed behavior is not optimal *relative to the particular model*. It is very, very difficult to prove conclusively that (inclusive) fitness would be significantly enhanced by some alternative, feasible behavior. As Maynard Smith (1978) has explained, it is not the hypothesis of optimality that is being tested, but simply the assumptions and structure of the model itself (see also Mitchell & Valone 1990). If a model's predictions are not upheld, it is the model that is rejected, not the paradigm of optimality. If optimization models fail repeatedly to explain observed phenomena, the optimality paradigm would have to be abandoned (provided a superior paradigm became available). The progression from individual, static optimization models to game-theoretic and dynamic models has been extremely successful in broadening the scope of optimality-based explanations.

One example in which nonoptimality appears to have been thoroughly demonstrated is nest parasitism; I thank **Colgan & Jamieson** for bringing the work of Rothstein (1982; 1986) to my attention. Whenever nonoptimal behavior seems so clearly established, the natural question concerns why more nearly optimal behavior has failed to evolve. I can think of only two possibilities: Either the apparently “optimal” behavior is not physiologically feasible (which is not the case for rejection of nest parasites, because some species of birds regularly reject), or the optimal behavior has simply failed to evolve. Rothstein (1986, p. 1117) asserts that “the lack of rejection behavior is a problem of evolutionary lag.” He points out (*ibid.*) that “brood parasitism is a more recent selective pressure than PCR [partial clutch reduction]. Birds or avian prototypes have, presumably, always been subject to PCR, whereas brood parasitism appeared only after the evolution of birds that switched from parental care to parasitism.”

This seems weak: Surely the switch to parasitism occurred in the distant past. It is not the total time, but the time integral of selection pressure that affects evolutionary changes. Terborgh (1989) points out that cowbird parasitism on North American passerines has vastly increased with the spread of agriculture, which provided feeding habitat for cowbirds. Before this recent development, selective pressure for defense against cowbird parasitism may have been minimal for forest-dwelling

species. To me this seems a more likely mechanism for evolutionary lag than that suggested by Rothstein (1986).

In any event, it is worth noting that even where optimality demonstrably fails, the optimality paradigm remains central to the discussion: if not optimal, why not?

Stamps points out that a whole sequence of models may be based on the same faulty, unrecognized underlying assumption. (She herself seems to make an unstated tacit assumption, namely, that lion "groups" are all of the same kind. In fact, hunting groups are not the same as social groups [prides]. There is no question that hunting group sizes are adjusted to available prey species and density.) This points up the necessity for modelers to criticize their assumptions and always to remain sensitive to the ways in which their predictions rely on the assumptions. Unfortunately, this is easier said than done – we all tend to be impressed by the brilliance of our arguments and to forget the importance of the underlying assumptions.

The assumption of complete information is a case in point; as Barto and Dickinson point out, this is frequently unrealistic. In principle, incomplete information and learning can be incorporated into dynamic programming models (which are then called adaptive control models), but the curse of dimensionality strictly limits the usefulness of this approach. The development of alternative modeling and computational techniques, such as incremental dynamic programming (Barto) and genetic algorithms (Miller & Todd, Houston & McNamara) is commendable. I don't know how fruitful these new techniques have been in expanding our understanding of observations of learning behavior. Hitchcock & Sherry correctly point out that learning involves much more than merely sampling the environment, which was the only sense in which I used the term in the target article.

Houston & McNamara indicate the possibility of linking behavioral models to the study of population dynamics. Most existing models of population dynamics completely ignore individual behavior, which may well have important consequences at the population level (McNamara & Houston 1987; Ydenberg 1987). This field of investigation has hardly been scratched.

3. Modeling for 'aha!'

I like simple models. I don't care if a simple, elegant model fails some statistical test (in this regard, contrast the commentary of Mace & Sutherland with that of Howe et al.), provided that it has given me some new ideas and insights into nature. It's always an exciting moment when a new model – especially one of my own – tells me, "Aha! So that's how it works." Calm reassessment in the light of data may later cause me to regret my naive enthusiasm, but not always – otherwise science would be an insufferable drudge.

I cannot resist the temptation here to describe a delightfully simple model, from Marc Mangel (1987), of oviposition strategy in parasitic wasps (see also Mangel & Clark 1988, Chapter 4). These wasps lay eggs in host pupae, and tend to lay larger clutches in larger hosts. A static model of Charnov & Skinner (1984), based on experimental measurements of the fitness of different sized clutches laid on hosts of different sizes, predicted a linear relationship between host volume v and optimal

clutch size $c^*(v)$. The data, however, consisted of a triangular cloud of points bounded sharply above by $c^*(v)$. Charnov & Skinner then proposed an alternative model, which predicted another line passing through the middle of the data.

Mangel developed a simple dynamic model, which on the first computer run reproduced the triangular cloud of points as its prediction. Mangel told me he was so surprised at this result that he spent the next three days looking for a bug in his program. But the program was correct, and the explanation (obvious by hindsight) soon emerged. The fitness curves measured by Charnov & Skinner were concave, with a maximum at $c^* = c^*(v)$. Clearly, if host pupae were available in unlimited numbers, it would be optimal for the parasite to lay one egg per host. (The clutch-size model used by Charnov & Skinner was carried over from avian studies, in which only one clutch at a time is laid and tended by the female parent. This tacit assumption is simply not valid for insects: Godfray 1987.) If host pupae are rare, the parasite may not be able to lay all its eggs in separate clutches, so larger clutches become optimal – but never larger than $c^*(v)$.

The variance in optimal clutch size was a consequence of Mangel's assumption that hosts were located by random search. Wasps that have been unlucky in locating hosts will lay larger clutches than those that have been more fortunate.

I am still charmed by the elegance and simplicity of Mangel's model. Not only does it predict what actually happens, while providing a convincing, simple explanation, but it also suggests all kinds of new experiments. (Not surprisingly, Mangel's paper was rejected by the first journal to which it was submitted.) For example, the manipulation of host density and spatial distribution have predictable, testable consequences. The same applies to manipulations affecting the parasites, for example, temperature changes affecting survival probabilities. Mangel and B. Roitberg are currently performing these experiments.

Was a dynamic programming model really necessary for understanding the triangular cloud? Maybe not, but it worked! My coworkers and I have repeatedly found that the process of developing a dynamic programming model has profoundly affected our thinking about the underlying biology (Ydenberg). This can only be appreciated by actually trying it. The fact that learning SDP modeling is easy also helps (other techniques, such as optimal control theory, are much more difficult to learn and to use).

4. The kitchen sink syndrome

The art of modeling always involves a compromise between simplicity and realism. Simple models are better, but so are more realistic ones. It is the easiest thing in the world to criticize a given model, or modeling approach, for being simplistic; I plead guilty to doing this relative to static models (Schmid-Hempel), and I likewise accuse many of the commentators of the same crime.

One school of modeling, to which Hitchcock & Sherry, Partridge, Milinski, and I do not belong, demands that models always encompass everything that might be important. This leads rapidly to "modeljunk" – useless

garbage piling up on office shelves (but fortunately unpublishable nowadays: Partridge). Unless we are careful, SDP models could also generate modeljunk.

As Mace & Sutherland point out, the limitations of SDP modeling may be more in the human brain than in computer capacity. How can anyone hope to comprehend multidimensional strategy matrices, depending on multidimensional state variables? I am happy to report some progress in this area. To understand the output of a model of induced defense strategies, we have recently developed 6-dimensional computer graphics (Clark & Harvell, unpublished).

Graphics is obviously the way to go in understanding data, whether empirical or model-generated. Six-dimensional graphs are not so arcane as might be supposed: One simply prints a folio of 3-dimensional graphs on a single page, organized across and down the page (5 dimensions), and iterated in perspective (the sixth dimension). Some thought is needed to achieve the most readable and informative output, but the method seems to be very efficient in terms of data comprehension. A Postscript laser printer is essential for high-resolution output (our graphs would cost a fortune to have drawn by an artist!).

A major shortcoming of SDP models is that the optimal strategies usually have to be obtained by computer. Studying the sensitivity of the predictions of such models to parameter values can be extremely tedious. Simpler models that can be solved analytically have great advantages, when they are possible. (I am much less sanguine about analytic models that can be solved only by professional mathematicians. It's essential for scientists to be able to work hands-on with their own models.)

In this regard, Sozou & Byrd have pointed out that Ydenberg's (1989) fledgling model, which I used as my expository example, can be solved without using dynamic programming (Odling-Smee also hints at this). They're quite right (although the forward simulation is only slightly simpler than backward iteration, in this case). Any stochastic model in which stochasticity is restricted to mortality risk is essentially equivalent to a deterministic model, which can often be solved analytically or by simulation (see also Ludwig & Rowe 1990). Ydenberg admits this, and also points out that his paper contains some ambiguities. I apologize to readers for uncritically using this example as my pedagogical device, but it does have the advantage of being easy to understand. (The referees of the first draft were horrified at the complicated example I used there.) The references in Table 2 contain many SDP models that cannot be solved without using dynamic programming – Mangel's oviposition model is one such.

By the way, Sozou & Byrd's statement that changing Ydenberg's (1989) terminal function to an exponential form completely changes the prediction of fledgling date might seem surprising without a little thought. But the reason for the difference is obvious: Ydenberg's function implies a linear advantage to weight gain above 700 g, whereas Sozou & Byrd's implies an asymptotic relation. Adult murres weigh about 950 gm. Ydenberg's assumption is that a 950 gm murre has a survival probability 2.5 times that of an 800 gm bird. Sozou and Byrd's function reduces this advantage to 1.5. Not surprisingly, then, Sozou & Byrd's chicks remain longer in the safety of the nest. How important is weight gain for murre chicks?

Ydenberg's model reveals that this could be an important question in studying the evolution of alcid fledgling behavior.

5. Miscellany

Adaptive variations. It is noted by Focardi that static models can predict averages but not variances. In a dynamic stochastic model, optimal behavioral strategies are state-dependent; the distribution of behaviors can be deduced from the distribution of the state variables. Mangel's oviposition model is a simple example of this.

In the case of fluctuating environments, it has long been recognized that the geometric mean of annual reproduction may be a better measure of fitness than the arithmetic mean. This has led to such concepts as bet hedging (Philippi & Seger 1989; Slatkin 1974) and adaptive coin flipping (Cooper & Kaplan 1982), in which phenotypic variation may be an adaptive strategy. Yoshimura & Clark (in press) show how to apply these ideas to dynamic programming models.

Nonadaptive variations. It is pointed out by Stamps that the optimum may be surrounded by a "zone of indifference" such that any behavior within the zone will lead to fitness that is close to the maximum. The selection pressure for reducing phenotypic variation (Colgan & Jamieson) within this zone of indifference will obviously be small. For this and other reasons one cannot expect too close quantitative agreement between predictions and observations. Although Townsend remarks that this may sometimes be used to rescue an unsuccessful theory, I feel it does have to be kept in mind.

The evolution of behavior. The question of how behavioral strategies evolve via the genetic system is not discussed in the target article. Travis points out that behavior is usually thought to be highly flexible (I presume he means genetically), in which case a blanket assumption of fitness maximization may be less problematic for behavioral than for, say, morphological traits. But as Szathmáry remarks, in the case of learned as opposed to inbred behavior, neuronal selection in the brain may be important. His suggestion that selfish neurons might compete with selfish genes to the detriment of fitness optimization is intriguing, but I have no idea how examples might be identified or tested. Maybe this should be added to the long list of "theory-rescue" devices to be invoked whenever a Darwinian explanation fails. My own preference is for model critique: If your model fails, try to figure out what's wrong with it. Only when all reasonable optimization models have failed do you have strong evidence for nonoptimal behavior (Rothstein 1982).

Matching. My facile remarks about matching are criticized by Fantino, Hitchcock & Sherry, and Houston & McNamara. I agree that matching would make a worthwhile dynamic modeling project. Regarding the observation that pigeons continue to match even after long experience with a nonchanging environment, I have two comments. First, given that reinforcements are randomized, how do the pigeons ever learn that the environment is constant? Humans regularly believe that luck comes in runs, why not pigeons? What are the statistical tests for the hypothesis of constancy, and how sophisticated would the pigeons have to be to use them? Second,

given that natural environments are never constant, how would pigeons ever evolve mechanisms for learning that their laboratory environment was in fact constant (Clark & Mangel 1986)?

Inclusive fitness. As noted in the target article, the assumption of individual optimization is quite unrealistic, given that the behavior of any organism is intimately linked with the behavior of predators and competitors. Behavior also often affects the fitness of offspring and other kin. Houston & McNamara point out the scope for dynamic ESS models. Miller & Todd think that dynamic programming cannot encompass inclusive fitness because of the assumption of a finite time horizon T . Ironically, the vast literature on ESS's and inclusive fitness is static, i.e., it assumes that $T = 1$! It must be a bit of an advance to allow for arbitrary finite T ; dynamic programming with an infinite horizon is treated in the literature (e.g., by Bertsekas 1987), but I'm not convinced that this would lead to much in the way of new insights in ecology.

(By the way, *BBS* authors are asked to rate the commentaries in terms of their favorability toward the target article, on a basis of 1 (high) to 7 (low). My average rating for the 22 commentaries was 2.4, which broke down as follows: psychologists 3.6 ($N = 6$), others 2.0 ($N = 16$). I also observed a similar bias among the commentaries on Houston & McNamara 1988. Do I infer that psychologists view the adaptationist paradigm with suspicion?)

Chaos. It is a concern of Partridge's that SDP models may exhibit extreme (chaotic) sensitivity to initial conditions, but his references concern only noncontrolled dynamical systems. I know of no theory of chaos for optimally controlled systems; my computer outputs have never suggested chaos. I also appreciate Townsend's comment on the current fad for chaos – it is an important paradigm shift, but it does not destroy all existing science.

Supporting theory. One of the advantages of the computer-oriented approach is that a minimum of theory is necessary (optimal control theory, a leading competitor, involves extremely complex and difficult theory pertaining to necessary and sufficient conditions for optimality). You just formulate your model and then program it for numerical solution. Townsend is worried about various technical problems involved in the numerical computations, but I have never encountered any serious difficulties. Discretization (in time and state) sometimes leads to jagged output, but this can be reduced by refining the mesh size, using interpolation, or adding additional stochastic noise. Stationary strategies almost always emerge for time-invariant models; I just watch the computer output as the number of iterations increases; see McNamara (1990) for theory.

6. Conclusion

Although dynamic optimization techniques have been around for quite a while, it is only recently that their usefulness in behavioral biology has been recognized. Experience with discrete-time, stochastic dynamic programming models of behavior has convinced me, as well as several colleagues, that such models are powerful, flexible, easy to learn and to use, and can yield rapid returns on investment. They seem particularly successful in helping us understand field and laboratory observa-

tions, and they often suggest new hypotheses and experiments. They can usually be implemented on desktop computers, further enhancing their attractiveness.

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