

A classification of dynamic optimization problems in fluctuating environments

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ABSTRACT

I consider how to classify and analyse models of the adaptive behaviour of an organism over a season. The classification is motivated by models of the timing of growth and reproduction in annual organisms, but applies to any model in which the population is unstructured at some convenient annual census time. During the season an organism makes a sequence of discrete behavioural choices. Each choice can be based on time in the season, any aspects of the organism's state, such as its size or energy reserves, and current environmental conditions. The organism may be subject to sources of demographic stochasticity that act independently on different population members. There may also be a source of environmental stochasticity, such as weather conditions that cause the environment as a whole to fluctuate. The classification of models given here is based on the types of stochasticity that act. I identify those models where the optimal strategy can be found simply by employing a dynamic optimization technique such as dynamic programming. For problems that are not solvable in this way, I outline other approaches that can be used to find a solution.

Keywords: allocation, dynamic programming, geometric mean fitness, growth, state dependence.

INTRODUCTION

Most organisms face a variety of uncertainties in their lives because of stochastic elements in the environment. Sources of stochasticity differ in the degree to which their effects are correlated across different individuals within a population. At one extreme, a source of *demographic* stochasticity acts independently on different individuals. For example, whether an animal is able to escape from a predator is due in part to luck. Furthermore, the death of one individual has little effect on whether a different population member dies within the same year. Thus 'luck in escape from a predator' can be regarded as a source of demographic stochasticity. At the other extreme, a source of *environmental* stochasticity has a highly correlated effect on all population members and can be thought of as causing the whole environment to fluctuate. For example, unpredictable fluctuations in temperature or rainfall affect all population members in the same way and are sources of environmental stochasticity. Typically, the food intake of an individual is influenced by both types of

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stochasticity: weather conditions or population density affect the overall level of food within the environment and are sources of environmental stochasticity; for a given level of overall food availability, the good or bad luck in finding food experienced by individuals is a source of demographic stochasticity. Here, I am concerned with a seasonal environment. Thus environmental conditions change over the course of a year. If these changes are the same each year, so that, for example, there is no year-to-year variation in the timing of seasons or in the harshness of winter, I refer to the environment as 'constant'. In a constant environment, organisms may experience demographic stochasticity but not environmental stochasticity. In contrast, in a 'fluctuating' environment, organisms are subject to environmental stochasticity due to year-to-year variation in conditions.

I assume that there is a season of growth and reproduction in each year. During this season an organism must make a sequence of behavioural choices. Here 'behaviour' includes growth and reproductive behaviour. Each choice can depend on the current time within the season, the organism's state and any information on the environment that is available. The strategy for choosing actions and the various sources of stochasticity determine the number of descendants left by the organism at the start of the next year. I discuss the appropriate measure of fitness for this scenario and show how to characterize and find the strategy that maximizes fitness. Much of the analysis is motivated and illustrated by models in which there is a trade-off between current reproduction and future growth, where future growing conditions are uncertain. Dan Cohen pioneered models of this type (Cohen, 1966, 1967, 1970, 1971). Here I use a model of reproductive effort in an annual plant (Amir and Cohen, 1990) to illustrate concepts and problems that arise.

FITNESS IN FLUCTUATING ENVIRONMENTS

For simplicity, I consider a species that is asexual. To define the fitness of a particular genotype of this species, assume that a census of genotype members is made at a succession of times that are one year apart. These census times are chosen at some biologically convenient time of year. Again for simplicity, I assume that members of the genotype are all in the same fixed state at every census; that is, the population is unstructured at census times. This is a reasonable assumption for many annual species. For example, consider a species that survives over winter only in the form of seeds or as eggs in diapause. During the summer, members of a genotype will differ in aspects of state, such as size, reproductive maturity and whether they are still growing or are already in a form to survive the winter. However, by taking the census at, say, midwinter, we ensure that all genotype members are essentially in the same state. The assumption may also be a reasonable approximation for species with overlapping generations providing that there are no substantial differences between different generations at the census times.

Consider a given individual that is present at a census time. Refer to this time as time 0 and refer to the next annual census time as time 0'. An organism present at time 0' will be referred to as a descendant produced by the focal individual between 0 and 0' if (1) the organism is the focal individual itself, (2) the organism is an offspring of the focal individual that was born between 0 and 0', or (3) the organism is in direct line of descent from an offspring of the focal individual, where the offspring was born between 0 and 0'.

The environmental conditions experienced by genotype members between two successive census times fluctuate from year to year as a result of environmental stochasticity. I describe environmental conditions in a given year by a vector, s , of attributes. This vector might, for

example, give the temperatures on all 365 days of the year. In addition to environmental conditions, which affect all genotype members equally, genotype members are affected independently by sources of demographic stochasticity. Consider a genotype member present at census time 0 and suppose that environmental conditions between 0 and the next census time $0'$ are s . Let $r(s)$ denote the expected number of descendants present at time $0'$ that are produced by this individual between 0 and $0'$; that is,

$$r(s) = E\{\text{no. of descendants produced over the year and still alive at the year's end}\}$$

where the expectation E denotes an average over demographic stochasticity for given environmental conditions s . Provided numbers of the genotype are large, the independent action of demographic stochasticity ensures that $r(s)$ is approximately equal to the annual proportionate growth in genotype numbers. The function r thus specifies how the growth in genotype numbers depends on environmental conditions. I refer to r as the profile of the genotype.

Let the random vector S denote environmental conditions in a randomly selected year. Then the fitness of the genotype is given by

$$g = E\{\log(r(S))\} \quad (1)$$

where E denotes an average over environmental stochasticity S (Lewontin and Cohen, 1969).

These concepts can be illustrated by the following two examples.

Example 1: Seed dormancy in an annual plant

Seed dormancy in fluctuating environments was first analysed by Cohen (1966). Here I present a simplified version of his model. An annual plant produces seeds in the autumn and then dies. The seeds fall to the ground where they join seeds that were produced by plants in previous years. At the beginning of the following spring, some of the seeds in the ground germinate and the remainder stay dormant during that growing season. In making the decision on whether to germinate, the seeds have no cues indicating subsequent growing conditions. Each growing season is either bad with probability $1 - a$ or good with probability a . If the growing season is bad, each germinating seed dies before it can grow into a mature plant. If the growing season is good, each germinating seed grows into a mature plant which then leaves y seeds in the ground at the beginning of the next spring. I assume that $ay > 1$ so that a growing seed leaves on average more than one descendant next year. A seed that remains dormant in spring decays before the start of the next spring with probability $1 - \beta$; this occurs independently of other seeds and the growing conditions that year. A genotype codes for the probability, p , that a seed germinates in spring; it is assumed that all members of a genotype germinate independently of one another.

For this model we take the annual census time to be just prior to any germination. At this time, all plants are present only as seeds in the ground and are essentially in the same state, so that the population is unstructured. There are three sources of stochasticity. Whether or not a dormant seed decays before next year and whether or not a seed germinates in spring are both sources of demographic stochasticity. The conditions during the growing season affect all population members and are a source of environmental stochasticity. There are two environmental conditions, $s = \text{'bad'}$ and $s = \text{'good'}$.

Consider a genotype with germination probability p . The profile r_p of this genotype is given by

$$r_p(\text{bad}) = (1 - p)\beta$$

and

$$r_p(\text{good}) = (1 - p)\beta + py$$

Both of the quantities are averages over all demographic stochasticity for given environmental conditions. The fitness of the genotype is then

$$g_p = (1 - a)\log[r_p(\text{bad})] + a\log[r_p(\text{good})]$$

The optimal germination strategy is for each seed to germinate with probability p^* , where p^* is the value of p that maximizes g_p . Differentiating g_p with respect to p and setting the derivative equal to 0 gives $p^* = (ay - \beta)/(y - \beta)$ (Cohen, 1966). This probability lies strictly between 0 and 1.

In this example, growing conditions in a year are a source of environmental stochasticity in that they affect all genotype members equally. To understand the optimal strategy, it is instructive to analyse an alternative model in which growing conditions are a source of demographic stochasticity, affecting genotype members independently. There is then no source of environmental stochasticity and environmental conditions are the same each year. Again consider the strategy of germinating with probability p . Since environmental conditions do not vary from year to year, the profile of a genotype that codes for this strategy is just a single number. I denote this constant by R_p . Averaging over all sources of demographic stochasticity, we have

$$R_p = (1 - a)r_p(\text{bad}) + ar_p(\text{good})$$

By formula (1) the fitness of this genotype is just $\log[R_p]$, since R_p is constant. This is maximized by maximizing R_p . As can be verified, this is achieved by setting $p = 1$. To understand this result, note that R_p is the expected number of descendants left next year by a randomly selected genotype member. Thus R_p is maximized by each genotype member maximizing the expected number of descendants that it leaves. A seed that germinates leaves on average ay descendants, whereas a seed that remains dormant leaves on average β descendants. Thus, since $ay > 1 > \beta$, a seed maximizes the expected number of its descendants by germinating immediately. In other words, when there is only demographic stochasticity $p^* = 1$.

In the above alternative model, during any year only some genotype members encounter bad growing conditions. In contrast, when growing conditions are a source of environmental stochasticity, all growing seeds die in bad years. Consequently, a genotype with germination probability $p = 1$ would be eliminated in the first bad year to occur. The strategy of germinating with probability $p^* < 1$ avoids such a catastrophic failure by diversifying the actions of genotype members. This strategy is an optimal compromise between maximizing descendant numbers and ensuring that at least some genotype members survive.

Example 2: The dependence of clutch size on territory quality

McNamara (1998) considers a model of clutch size in birds in which nesting birds have a range of territory qualities. In the model, each bird knows its own territory quality and

must choose its clutch size before weather conditions during brood provisioning are known. Certain types of territories are more strongly affected by bad weather than others. Furthermore, large clutches are more susceptible than small clutches to a complete nest failure.

Let $d(x, c, s)$ denote the expected number of descendants left next year by a bird that has a territory of quality x and produces a clutch of size c , given that weather conditions during provisioning are s . A strategy specifies the dependence of clutch size $c(x)$ on territory quality x . First suppose that all sources of stochasticity, including weather, are demographic. Then, the fitness of a genotype that codes for the strategy $c(x)$ is $\log(R)$ where

$$R = E\{d(X, c(X), S)\}$$

Here, the random variable X denotes the quality of a randomly selected territory and the expectation is an average over both X and weather conditions S . R is the average number of descendants left by a genotype member and is maximized if each individual bird maximizes the expected number of descendants left. That is, a bird with territory of quality x should choose c to maximize $E\{d(x, c(x), S)\}$, where the expectation is an average over S .

Now suppose that weather is a source of environmental stochasticity. Then, the profile of a genotype that codes for strategy $c(x)$ is

$$r(s) = E\{d(X, c(X), s)\}$$

where the expectation is an average over territory quality X for given weather conditions s . The fitness of the genotype is then given by expression (1). In this case, the optimal clutch size on a territory of given quality depends on the distribution of territory qualities in the environment as a whole. To understand this result, consider behaviour on a territory type that is strongly and adversely affected by bad weather. If all genotype members have this type of territory, then some should produce small clutches to guard against a catastrophic failure for the genotype as a whole. Conversely, if most genotype members have territories that are little affected by adverse weather, then genotype members on the type that is sensitive to weather conditions can afford to take risks by producing large clutches, since even if all of these fail others will not.

COMPARISON OF OPTIMIZATION IN CONSTANT AND FLUCTUATING ENVIRONMENTS

The above examples can be used to illustrate some crucial differences between optimal behaviour when there is no environmental stochasticity (i.e. a constant environment) and fluctuating environments. As before, all remarks pertain to scenarios in which the population is unstructured at the annual census times.

Maximization of descendant numbers

In a constant environment, every individual behaves so as to maximize the expected number of descendants left at the census time next year (where the expectation is an average over demographic stochasticity). Typically in a fluctuating environment, individuals do not maximize expected descendant number (where the expectation is an average over both environmental and demographic stochasticity).

Individual optimization and implicit frequency dependence

In a constant environment, the optimal behaviour of an individual can be specified without reference to the states or actions of other genotype members. This is because the fitness of the genotype is maximized if every genotype member maximizes the expected number of descendants that it leaves. The following stronger version of this result also holds. Suppose that we constrain some members of a genotype to perform specified, possibly sub-optimal, actions; for instance, in Example 2, we might constrain clutch sizes on certain types of territories. Then, given this constraint, the fitness of the genotype is maximized by remaining genotype members each maximizing expected descendant number.

In a fluctuating environment, it is possible to consider individuals in isolation only in special cases. The seed germination model is such a case. When the decision whether to germinate is made, all genotype members are in the same state. The strategy adopted by one (in this case specified by the probability of germination) is then representative of all. Consequently, fitness is maximized by each genotype member maximizing the expected logarithm of the number of descendants left next year. However, even in this case, the above stronger form of individual optimization does not hold. To see this, suppose that almost all seeds are constrained to germinate in a year. Then it is best for the genotype if the rest remain dormant. Conversely, if almost all seeds remain dormant, it is best for the remainder to germinate. McNamara (1995) refers to this dependence on the behaviour of other genotype members 'as implicit frequency dependence'.

When individuals of a genotype differ in some aspects of state when a decision is made, there is no individual optimization even in a weak sense. This is illustrated by Example 2. In this example, fitness is maximized by the collective action of genotype members maximizing the expected logarithm of the number of descendants left next year, but in this example this is not achieved by each individual maximizing the expected logarithm of the number of descendants that it leaves. Furthermore, nothing else is maximized in isolation, since the optimal clutch size on a territory depends on the distribution of territory qualities in the environment as a whole.

Randomized strategies

In constant environments, no randomized strategy (that is, a strategy in which actions are chosen probabilistically) can perform strictly better than the best deterministic strategy. As the seed germination example shows, this is not true in fluctuating environments.

DYNAMIC OPTIMIZATION

The discussion so far has been illustrated by examples in which an organism makes a single decision each year, but the concepts apply to any scenario where there is a sequence of decisions over the year. For the remainder of the paper, I focus on such dynamic optimization problems. Suppose that in each year there is a growing season that starts at time 0 and ends at or before time T . At each of the times $t = 0, 1, 2, \dots$, an organism must make a behavioural choice. Each action chosen results in an immediate contribution to the reproductive success of the organism. It also affects the state of the organism at the next decision epoch, and hence affects future reproductive success. There may therefore be a trade-off between current and future reproductive success within the season. Both the choice of action and the consequences of this choice may depend on the time within the season,

the organism's state and environmental conditions. Consequences may also be subject to demographic and environmental stochasticity. Under an optimal strategy behaviour again maximizes expression (1).

Regardless of the type of stochasticity, in dynamic optimization problems the best action of an individual at a given time depends on its state and future expectations. Future expectations depend in part on the future choices made by the individual. Thus, to find the optimal action at a given time, it is necessary to first find the optimal strategy at all future times in the season. Because of this logic, an obvious approach is to start at the end of the season (time T) and work backwards using an approach such as dynamic programming. Some problems can be solved by dynamic programming alone, others cannot. My main purpose in this paper is to characterize the various sorts of problems that can arise and to expose the logic behind their solution. The fundamental difference between different cases can be summarized as follows.

- A. *Demographic stochasticity alone.* As in Examples 1 and 2, when there is no environmental stochasticity each individual maximizes the expected number of descendants left next year. The strategy that achieves this maximum can be found simply by working backwards using dynamic programming.
- B. *Environmental stochasticity but no demographic stochasticity.* Suppose that the following three conditions hold:
 - (i) All members of a genotype are in the same state at time 0.
 - (ii) There is no demographic stochasticity.
 - (iii) Genotype members follow a deterministic strategy.

Then all individuals will be in the same state as one another at each subsequent time in the season. Thus, as in the seed germination model, what happens to one individual in a given year represents what happens to all genotype members within that year. Then, provided assumptions (i)–(iii) hold for the optimal genotype, each member of this genotype behaves to maximize the expected logarithm of the number of descendants that it leaves next year. This behavioural strategy can be found by dynamic programming.

- C. *Environmental and demographic stochasticity.* Suppose that at least one of assumptions (i)–(iii) fails. Then there will be a time t in the season when members of the genotype will be in a range of states. The best action of an individual at this time implicitly depends on this distribution of states of relatives. But this distribution depends on the behavioural strategy followed by genotype members before time t . Thus, it is not possible to specify optimal behaviour at time t until optimal behaviour has been specified at all previous times as well as future times. The optimal strategy cannot now be found by simple dynamic programming.

The difference between problems of types (B) and (C) is that, when assumptions (i)–(iii) hold, the state of an individual at time t specifies exactly the states of relatives (since all genotype members are in the same state), whereas when one of these assumption fails, the states of relatives can only be reconstructed from knowledge of their previous behaviour.

Previous attempts to solve problems of type (C) by simple dynamic programming have been flawed because relatives have been ignored. For example, Yoshimura and Clark (1991) assumed that there is individual optimization with each genotype member maximizing the

expected logarithm of the number of descendants left: an assumption valid for problems of type (B) but not type (C).

The above classification of problems is illustrated by the following example.

ALLOCATION TO GROWTH AND REPRODUCTION IN AN ANNUAL PLANT

This example is concerned with the allocation of resources to growth and reproduction in an annual plant during a growing season of unpredictable length. The model is based on that of Amir and Cohen (1990), but with minor changes to details of the model and a different terminology.

It is convenient to divide the growing season into a sequence of discrete days, where time t is the start of day t . The season starts at time 0 and ends at or before time T . At time t , the physiological state of a plant is characterized by the size of its vegetative part, x_t , and the size of its reproductive part, y_t . Growing conditions may vary from day to day. I denote growing conditions on day t by s_t . If the growing season has not ended by time t , the plant grows during that day. The total resources acquired via photosynthesis during the day, $k(x_t, s_t)$, depends on the size of its vegetative part and growing conditions. The plant chooses how it allocates resources between growth of the vegetative part and growth of the reproductive part. Denoting the allocations to these parts by Δx and Δy , respectively, we thus have

$$x_{t+1} = x_t + \Delta x$$

and

$$y_{t+1} = y_t + \Delta y$$

where Δx satisfies the constraint

$$0 < \Delta x < k(x_t, s_t) \quad (2)$$

and where

$$\Delta x + \Delta y = k(x_t, s_t) \quad (3)$$

The growing season is of variable length. For simplicity, we can suppose that the season ends at one of the decision epochs $0, 1, \dots, T$, rather than part way through a day. If the season has not ended by time t , then it ends at time $t+1$ with probability H_t . Since the season always ends by time T , we have $H_{T-1} = 1$. The number of descendants left next year by a plant is taken to be equal to the size of its reproductive part when the season ends. Let τ denote the time at which the season ends and let $s = (s_0, s_1, s_2, \dots, s_\tau)$ be the vector of growing conditions during the season. Then, emphasizing that the size of the reproductive part at the end of the season depends on both growing conditions and season length, I denote this size by $y_\tau^*(s)$.

In this model, there are two sources of stochasticity, namely growing conditions, s , and season length, τ . The optimal strategy depends crucially on whether sources of stochasticity are environmental or demographic. I examine three cases.

Case I: No environmental stochasticity

Assume that the growing conditions and season length experienced by different individuals are independent. All stochasticity is thus demographic and, under an optimal strategy, each

plant behaves to maximize the expected size of the reproductive part at the end of the growing season. That is, it maximizes

$$R = E\{y_\tau^*(s)\} \quad (4)$$

where the expectation is an average over both τ and s .

Consider a plant that follows the optimal strategy. Let $V(x_t, y_t, s_t, t)$ denote the expected size of the reproductive part of this plant at the end of the season, given that, at time t , the plant has vegetative part of size x_t , reproductive part of size y_t and growing conditions are s_t . Then, V satisfies the dynamic programming equation

$$V(x_t, y_t, s_t, t) = \max\{H_t(y_t + \Delta y) + (1 - H_t)E[V(x_t + \Delta x, y_t + \Delta y, S_{t+1}, t + 1)]\} \quad (5)$$

where the expectation is an average over possible values of the growing conditions at time $t + 1$. Here the maximization is over all possible Δx and Δy satisfying constraints (2) and (3). Given that V satisfies the terminal condition

$$V(x_T, y_T, s_T, T) = y_T$$

we can work backwards over the season using equation (5) to find $V(x_t, y_t, s_t, t)$ for all x_t , y_t , s_t and t .

These equations can be reformulated by noting that the final size of the reproductive part is just the sum of the growth increments in each time unit. Because of this we can set

$$V(x_t, y_t, s_t, t) = W(x_t, s_t, t) + y_t$$

where $W(x_t, s_t, t)$ is the expected future growth of the reproductive part from time t onwards. The dynamic programming equations for W are then

$$W(x_t, s_t, t) = \max\{\Delta y + (1 - H_t)E[W(x_t + \Delta x, S_{t+1}, t + 1)]\}$$

and

$$W(x_T, s_T, T) = 0$$

Case II: No demographic stochasticity

I now assume that, at any time in the season, all members of a genotype experience the same growing conditions as one another. I also assume that the growing season is the same length for all genotype members. Finally, I assume that all members of the genotype have the same sizes of vegetative and reproductive parts at time 0. Then, provided that genotype members follow a deterministic growth strategy, there is no demographic stochasticity and all stochasticity is environmental. The profile for the genotype is then

$$r(s, \tau) = y_\tau^*(s)$$

Suppose that the optimal strategy is deterministic. By expression (1) this strategy maximizes

$$g = E\{\log[y_\tau^*(S)]\} \quad (6)$$

where the expectation is over both S and τ . Consider a plant that follows this optimal strategy. Let $V(x_t, y_t, s_t, t)$ denote the expected logarithm of the size of the reproductive part of this plant at the end of the season, given that, at time t , the plant has vegetative part of size x_t , reproductive part of size y_t and growing conditions are s_t . Thus, the difference

between V here and the V for Case I is that we are now taking logarithms before averaging. This new V satisfies the dynamic programming equation

$$V(x_t, y_t, s_t, t) = \max \{ H_t \log(y_t + \Delta y) + (1 - H_t) E[V(x_t + \Delta x, y_t + \Delta y, S_{t+1}, t + 1)] \} \quad (7)$$

where, as before, the expectation is an average over possible values of the growing conditions at time $t + 1$ and the maximization is over all possible Δx and Δy satisfying constraints (2) and (3). Given that V satisfies the terminal condition

$$V(x_T, y_T, s_T, T) = \log(y_T)$$

we can work backwards over the season using equation (7) to find $V(x_t, y_t, s_t, t)$ for all x_t, y_t, s_t and t .

As in Case I, these equations can be reformulated. Set

$$V(x_t, y_t, s_t, t) = W(x_t, s_t, t) + \log(y_t)$$

where $W(x_t, s_t, t)$ is the expected future logarithmic growth of the reproductive part from time t onwards. The dynamic programming equations for W are then

$$W(x_t, s_t, t) = \max \{ \log[(y_t + \Delta y)/y_t] + (1 - H_t) E[W(x_t + \Delta x, S_{t+1}, t + 1)] \}$$

and

$$W(x_T, s_T, T) = 0$$

(Amir and Cohen, 1990).

The allocation to growth and reproduction over a season of variable length is also considered by King and Roughgarden (1982). In their model, there is also environmental stochasticity but no demographic stochasticity and the optimal strategy can be found by the application of a suitable dynamic optimization technique. However, in this model, allocation decisions are made at a continuum of times rather than at a discrete set of times and the optimization technique employed is Pontryagin's maximum principle rather than dynamic programming.

Case III: Environmental and demographic stochasticity

Assume that individuals experience independent growing conditions, so that this is a source of demographic stochasticity. All individuals experience the same season length in a given year, so season length is a source of environmental stochasticity. For this scenario, the profile of a genotype is

$$r(\tau) = E[y_\tau^*(S)]$$

where the expectation is an average over growing conditions S for fixed season length τ . By expression (1) an optimal strategy maximizes

$$g = E\{\log(E[y_\tau^*(S)])\} \quad (8)$$

where the inner expectation is an average over the source of demographic stochasticity S and the outer expectation is an average over the source of environmental stochasticity τ . This is a dynamic optimization problem of type (C) of the previous section. For the reasons given there, it cannot be solved by simple dynamic programming. A comparison of

expressions (4), (6) and (8) shows directly why this case is more difficult to analyse than Cases I and II: the double expectation in expression (8) makes Case III far more complex. I now describe methods by which such complex optimization problems can be solved.

GENERAL OPTIMIZATION METHODS

This paper is concerned exclusively with genotypes which are unstructured at a suitable annual census time and have fitness measure given by expression (1). The dynamic optimization problems considered look for optimal behaviour between two consecutive census times. Here I summarize methods available for the solution of such problems.

If a strategy can be specified by just a few parameters, it may be possible to find the optimal strategy by simply maximizing over the parameters. For example, in the model of brood reduction of Temme and Charnov (1987), a bird has to make two decisions. Clutch size is chosen before environmental conditions during provisioning are known. Once the eggs hatch, the bird discovers whether environmental conditions during provisioning are good or bad; if bad, the bird chooses the amount of brood reduction. For this model, a strategy is specified by just two parameters – clutch size and the amount to reduce the brood if bad. Temme and Charnov give an expression for fitness in terms of these parameters and hence find the optimal strategy by simple differentiation. Amir and Cohen (1990) also used a static optimization approach to analyse one of their models.

Typically, however, dynamic optimization problems are far too complex for the above static optimization approach to be feasible, especially when individuals can be in one of several states at each of the times. I have indicated above what types of problems may be solved by dynamic programming alone. I now outline two general methods by which a solution to any dynamic optimization problem of arbitrary complexity can, in principle, be found. However, as I discuss in the next section, these methods yield a solution to the unconstrained problem, whereas it may be more biologically realistic to solve a particular constrained optimization problem.

First method: Control of the structure vector

Suppose that individuals of a genotype can be classified as being in one of K states labelled $x = 1, 2, \dots, K$. At any given time, members of the genotype may be in a range of these states. Let $N_x(t)$ = the number of genotype members in state x at time t , and let $N(t)$ be the vector of numbers given by $N(t) = (N_1(t), N_2(t), \dots, N_K(t))$. Then this vector summarizes information on the genotype at time t . The sequence of vectors $N(0), N(1), \dots, N(T)$ specifies how numbers of genotype members in each of the states changes over the season. Equivalently, N can be re-expressed in terms of total number of genotype members and the vector giving proportions in each state. I refer to this latter vector as the structure vector for the genotype. The collective action of genotype members can be viewed as controlling the proportionate increase in absolute numbers and the change in the structure vector over each time unit. This approach reduces the optimization problem to a standard optimal control problem that can be solved using a technique such as dynamic programming. I refer to the method as control of the structure vector.

The method just described is very general and can be applied to all cases where there is environmental stochasticity. However, in Case II of the previous section, the structure vector is degenerate, since all individuals of the genotype are in the same state as one

another at each time. It is then easier to make use of this fact and take the approach outlined in the previous section rather than the current approach. When individuals of the genotype are in a range of states at a given time, as in Case III, the structure vector is not degenerate and, as the following example illustrates, the present approach may be worthwhile.

Many species go through a sequence of discrete generations over a growing season of variable length. This season ends due to an adverse change in environmental condition brought about by factors such as weather, food or predators (e.g. Tauber *et al.*, 1986; Hairston, 1987). At the end of the growing season, only individuals already in a diapause state survive through to the next season. In the model of McNamara (1994), there may be many generations over the growing season but the time of completion of each generation is fixed. This model is analysed by converting the problem into one of optimal control of the structure vector. To do so, time t is defined as the time of completion of generation t . At this time, individuals are in one of two states: eggs already in diapause from previous generations or newly produced eggs. The parent controls whether a newly produced egg immediately enters diapause until next year or grows to produce more eggs on maturity. The collective action of genotype members at t then determines numbers of individuals in the two states at the end of the next generation – that is, determines the structure vector at time $t + 1$. An optimal strategy for this control problem specifies how the proportion of eggs entering diapause depends on the time t and the current value of the structure vector. McNamara gives an analytic expression for this strategy. To predict optimal behaviour under this strategy, a cohort comprising individuals present at the start of the season and their descendants later on in the season is followed over a season. This gives the structure vector of the cohort at each time in the season. The value of this vector at time t and the optimal strategy then combine to give the proportion of all eggs produced by cohort members at t that immediately enter diapause.

Although both methods presented in this section can be used to solve diapause-type problems, other methods have also been used. Optimal entry into diapause was first modelled by Cohen (1970). In his model, there are just two generations but the time of completion of the first generation is variable. Cohen analyses the model by expressing fitness in terms of a set of parameters and maximizing over these parameters.

To apply the structure vector method to Case III of the previous section, one would first make the approximation that the possible sizes of the vegetative and reproductive parts of a plant fall into one of a number of discrete categories. The structure vector would then specify the proportion of a given genotype in each of these categories. Unfortunately, unless there are a very small number of size categories, the structure vector is of high dimensionality. It is then not feasible to solve the dynamic programming equations by numerical computation because of demands on computer memory and time. Instead, an approach such as the following must be used.

Second method: Convert the problem into a game

In a fluctuating environment, the best action of one individual implicitly depends on the actions of other genotype members. McNamara (1995) used this idea to reformulate any optimization problems in a fluctuating environment as a constant environment game. Specifically, in that paper, I show that a strategy maximizes expression (1) if, and only if, it is an equilibrium solution to the corresponding game. By equilibrium solution I mean a

strategy that is the best response to itself. The motivation behind this result is that an optimal strategy has the property that, if almost all members of a genotype follow the strategy, it is best for the genotype if the remaining genotype members also follow this strategy.

The advantage of this reformulation is that the best response to a given strategy maximizes an appropriate measure of the expected number of descendants left next year, rather than the logarithm of expected descendant number. The problem of finding the best response is, therefore, equivalent to finding an optimal strategy when there is no environmental stochasticity. Such a strategy can always be found by dynamic programming. Although finding the best response to a given strategy is easy, it may not be so easy to find a strategy that is the best response to itself. As with dynamic games, the obvious iterative techniques may not always give the required solution (McNamara *et al.*, 1997).

This game-theoretic approach to solving dynamic optimization problems is illustrated by McNamara *et al.* (1995). In their model, an animal builds up its energy reserves over a fixed time interval. During that interval, the animal is subject to demographic stochasticity in its foraging gains. The animal's energy reserves at the end of the interval and the ensuing environmental conditions (which vary unpredictably) determine the number of descendants left next year. In the reformulation of this model as a game, a given strategy determines a function that specifies the 'value' of the energy reserves accumulated by the end of the interval. The best response to the given strategy is then the strategy that maximizes this expected value. This best response can be found by dynamic programming, taking the function specifying value as the terminal reward.

The model of McNamara *et al.* (1995) is similar to Case III of the previous section in that in both models only demographic stochasticity acts during the period in which behaviour is analysed. The main difference between the models is that, in the model of plant growth, the season length is variable and conditions after the end of the season are fixed, whereas in the model of McNamara *et al.*, the season length is fixed and conditions vary after the season. The game-theoretic approach is well suited to both models and avoids the problems of dimensionality inherent in the structure vector approach.

INDIVIDUAL AND POPULATION-BASED STRATEGIES

I have emphasized that, when there is environmental stochasticity, there is implicit frequency dependence between members of the same genotype. In particular, the best action of an individual depends on the states of relatives at this time. Thus, an optimal strategy specifies the action of an individual as a function of time, its own current state and the current structure vector for the genotype. Following McNamara (1997), I refer to a strategy as *population-based* if behaviour can depend on the current structure vector and refer to a strategy as *individual-based* if behaviour is constrained to depend only on time and on an individual's current state. Individual-based strategies are thus a subset of the class of population-based strategies. In most circumstances, it does not seem reasonable to allow individuals to have direct knowledge of the states of relatives. Thus, it could be argued that we should seek the best strategy within the restricted class of individual-based strategies. Unfortunately, both general methods outlined in the previous section find the best strategy in the wider class of population-based strategies.

The above does not always present a problem. For example, consider Case II of the model of allocation for an annual plant. Because of a lack of demographic stochasticity in this

model, all individuals are in the same state at a given time. Thus, the structure vector is specified by the state of an individual and the optimal population-based strategy is also individual-based.

For many problems, the best population-based strategy is realizable if genotype members follow an appropriate individual-based strategy. For example, consider the model of timing of entry into diapause of McNamara (1994) that is described in the previous section. There, the optimal strategy is found by the approach based on control of the structure vector. Under this strategy, the best action of an individual depends explicitly on the current value of the structure vector. Thus, the strategy is population-based but not individual-based. However, if a cohort of individuals follows the strategy, the structure vector for the cohort changes deterministically between successive time points. Thus, given an initial structure vector at time 0, the structure vector at each subsequent time can be specified. Therefore, rather than specifying behaviour of cohort members in terms of time and the structure vector, it is possible to produce the same behaviour by responding to time alone.

In the diapause example, there is no environmental stochasticity during the period in which individuals make decisions. Consequently, under the optimal strategy, the structure vector is uniquely determined by the time and need not be observed directly (cf. Collins and McNamara, 1998). This reasoning would also apply to Case III of the model of allocation for an annual plant. However, if there had been both environmental and demographic stochasticity during the growing season, the structure vector could not be expressed in terms of time alone, but would depend on past growing conditions. The optimal strategy would not then be realizable by individuals responding to their own state and to time and a genotype whose members could explicitly respond to past growing conditions would have selective advantage over a genotype whose members could not.

Although some work has been done on finding the best individual-based strategy when this differs from the best population-based one (McNamara, 1997), this area needs further development.

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