

## **Solution of functional difference equations from behavioral theory**

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**Abstract.** Behavioral models based on Markovian decision processes lead to functional difference equations for quantities such as the mean lifetime of the forager and the probability of reproductive success of the forager. In this paper, asymptotic and iterative methods are developed for the solution of such equations. The asymptotic methods are compared with numerical simulations. The iterative methods can be proved by a simple application of contraction mapping theorems.

**Keywords:** Foraging — Behavioral ecology — Asymptotic methods

### **1. Introduction**

Recently, Mangel and Clark (1986) introduced a theory of behavior called unified foraging theory (UFT) which provides a consistent way for modeling three major aspects of behavior: finding food, avoiding predation, and reproducing. UFT is based on the theory of Markov decision processes and involves the solution of various stochastic dynamic programming equations (SDPs). For example, one of the paradigmatic problems in foraging theory is the problem of patch selection. It is treated in UFT in the following way. One begins by identifying a suitable state variable  $X(t)$  which characterizes the (energetic) state of the forager at the start of period  $t$ . The  $i$ th patch is characterized by these variables:

$$\begin{aligned}\beta_i(x) &= \text{Prob}\{\text{suffering predation in the } i\text{th patch between } t \\ &\quad \text{and } t+1 \mid X(t) = x\} \\ \alpha_i(x) &= \text{energetic cost of foraging in the } i\text{th patch when } X(t) = x. \\ \lambda_{ij}(x) &= \text{Prob}\{\text{finding food type } j \text{ in the } i\text{th patch between } t \\ &\quad \text{and } t+1 \mid X(t) = x\}\end{aligned}\tag{1}$$

$Y_{ij}$  = energetic value of food type  $j$  in the  $i$ th patch

(For most of this paper, a discrete time formulation is used. This is done mainly for pedagogic convenience. In the last section, the methods developed here are

applied to continuous time problems.) The dynamics of  $X(t)$  are then modelled in the following way. If the forager chooses to forage in the  $i$ th patch in period  $t$ , then with probability  $\beta(X(t))$  the forager is killed by a predator with the probability  $1 - \beta(X(t))$

$$X(t+1) = X(t) - \alpha_i(X(t)) + \tilde{W}_i \quad (2)$$

where  $\tilde{W}_i$  is a random variable such that

$$\begin{aligned} \Pr\{\tilde{W}_i = Y_{ij}\} &= \lambda_{ij}(X(t)) \\ \Pr\{\tilde{W}_i = 0\} &= 1 - \sum_j \lambda_{ij}(X(t)). \end{aligned} \quad (3)$$

In many cases, it is reasonable to add a capacity constraint,  $C$ , so that  $X(t+1) = C$  if the right-hand side of (2) exceeds  $C$  and  $X(t+1)$  is given by (2) otherwise.

Mangel and Clark (1986) used this formulation to analyze both the probability of survival and expected fitness when reproduction within each period is possible. For example, one can define

$$p(x, t, T) = \max \text{Prob}\{\text{survival to time } T \mid X(t) = x\} \quad (4)$$

where death can occur either by predation or by  $X(t)$  falling below a critical, starvation level  $x_c$ . It can be shown that  $p(x, t, T)$  is the solution of a stochastic dynamic programming equation (see Mangel and Clark 1986 for details) which is easily solved by numerical iteration between periods  $t$  and  $t-1$ . The same is true if (4) is replaced by

$$F(x, t, T) = \max E\{f(X(T)) \mid X(t) = x\} \quad (5)$$

where  $f(x)$  is the fitness associated with the level  $x$  at the time when fitness is assessed. That is,  $F(x, t, T)$  is the maximum expected fitness at time  $T$ , conditioned on  $X(t) = x$ .

The purpose of this paper is to develop methods for solving a conceptually different equation that characterizes the mean lifetime of the forager. There are a number of reasons for studying this lifetime equation, other than its inherent mathematical interest. For example, if the forager represents a pest, then the mean lifetime characterizes the average length of the infestation. If the forager accrues fitness which is related to the length of its life, then the mean lifetime is a proxy for fitness.

The same methods which are developed for the lifetime equation can be applied to the problem of computing the probability of reproductive success of a "sit-and-wait" predator (see, e.g. Arnold (1978), Caraco and Gillespie (1985), Huey and Pianka (1981), Olive (1982) or Winterhalder (1983) for a discussion of the ecological and modeling issues associated with a sit-and-wait predator).

In this next section, the mean lifetime equation is derived. It is solved, by asymptotic methods, in the third section for the case of always foraging. In the fourth section an iterative solution for the mean lifetime equation is given and the advantages of foraging optimally are discussed. In the fifth section, the methods developed in Sects. 3 and 4 are applied to compute the probability of reproductive success of a set-and-wait predator. Finally, Sect. 6 contains conclusions and a discussion of other applications of the method.

## 2. Formulation and derivation of the lifetime equation

Define  $T(x)$  by

$$T(x) = \max E\{s: X(s) \leq x_c \text{ or the forager dies by predation} | X(0) = x\}. \quad (6)$$

It is then clear that one condition that  $T(x)$  satisfies is

$$T(x) = 0 \quad \text{for } x < x_c. \quad (7)$$

The behavior of  $T(x)$  at  $x_c$  depends upon the local behavior of  $X(s)$  near  $x_c$ . If  $X(s)$  can jump across  $x_c$  (from a value greater than  $x_c$  to one less than  $x_c$ ) then, in general, no condition can be placed on  $T(x_c)$  and  $T(x)$  may be discontinuous at  $x_c$  (see, e.g. Knessl et al. (1986) for a discussion of this point). This will be called case *J* (for jump). If, on the other hand,  $X(s)$  smoothly passes through  $x_c$  as it decreases below  $x_c$ , then the condition  $T(x_c) = 0$  is appropriate. This will be called case *C* (for continuous). For many problems analyzed by UFT, one can develop a formulation in which  $X(s)$  is a random walk on a lattice with single steps towards the left, so that  $T(x_c) = 0$  is appropriate.

The equation that  $T(x)$  satisfies is derived as follows. Suppose that the forager chooses the  $i$ th patch when  $X(0) = x$ . The following is assumed: (1) With probability  $\beta_i(x)$  it lives only one period (in which it is implicitly assumed that the forager is credited with one unit of time regardless of when the predation occurs). (2) With probability  $(1 - \beta_i(x))\lambda_{ij}(x)$  the forager lives one period and starts the next period with state variable  $x = \alpha_i(x) + Y_{ij}$ . Thus,  $T(x)$  satisfies

$$T(x) = \max_i \left[ \beta_i(x) + (1 - \beta_i(x)) \left( 1 + \sum_j \lambda_{ij} T(x_{ij}) \right) \right] \quad (8)$$

where  $x_{ij} = \min[x - \alpha_i(x) + Y_{ij}, C]$ . Equation (8) is the nonlinear functional difference equation for  $T(x)$ .

It is worthwhile to consider a special case of (8) which has no effect on the validity of the solution methods but leads to considerable additional intuition. In this special case, there are only two patches. One corresponds to hiding (subscripted *h*) with  $\beta_h \equiv 0$ ,  $\lambda_{ij} \equiv 0$  and  $\alpha_h$  given. In the second patch, there is only one type of food, with energetic value  $Y$ , which is found with probability  $\lambda(x)$  and the energetic cost of foraging in  $\alpha_f$ . Setting  $x' = \min[x - \alpha_f(x) + Y, C]$  and using this in the simplified version of (8) gives

$$T(x) = \max[ T(x - \alpha_h), \beta_f(x) + (1 - \beta_f(x)) [1 + \lambda T(x') + (1 - \lambda) T(x - \alpha_f)] ]. \quad (9)$$

Simplifying (9) gives

$$T(x) = \max[ T(x - \alpha_h), 1 + (1 - \beta_f(x)) \{ \lambda T(x') + (1 - \lambda) T(x - \alpha_f) \} ]. \quad (10)$$

Most of the methods reported here will be illustrated using (10) rather than (8) simply because it is easier to see what is going on.

### 3. Asymptotic solution for the case of always foraging

In this section, the lifetime equation is solved when the animal always forages. In that case, the mean lifetime  $T(x)$  satisfies

$$T(x) = 1 + (1 - \beta_f(x))\{\lambda(x)T(x') + (1 - \lambda)T(x - \alpha_f)\}. \quad (11)$$

To begin, assume that  $\beta_f(x)$  and  $\lambda(x)$  are constants. Then, if  $x$  is large assume

$$T(x) \sim T_0 \quad \text{for } x \text{ large.} \quad (12)$$

Substituting  $T_0$  for  $T(\cdot)$  in (11) gives

$$T_0 = 1 + (1 - \beta_f)\{\lambda T_0 + (1 - \lambda)T_0\} \quad (13)$$

with solution

$$T_0 = \frac{1}{\beta_f}. \quad (14)$$

The interpretation of (12)–(14) is straightforward. For large initial values of the state variable, the lifetime of the forager is determined mainly by predation—so the lifetime is the expectation of a geometric random variable. The value  $T_0 = 1/\beta_f$  which is asymptotic to  $T(x)$  for large  $x$  is the outer solution in the parlance of matched asymptotic expansions (Kervorkian and Cole (1981), Knessl et al. (1984), Matkowsky et al. (1984)). It does not satisfy the boundary condition  $T(x) = 0$  for  $x < x_c$  (case *J*) or  $T(x) = 0$  for  $x \leq x_c$  (case *C*). In order to do that, assume that

$$\begin{aligned} T(x) &= T_0(1 - A e^{-\gamma x}) \\ &= \frac{(1 - A e^{-\gamma x})}{\beta_f} \end{aligned} \quad (15)$$

where  $\gamma$  is a constant to be determined and  $A \equiv 1$  for case *C* and  $A$  must be determined for case *J*.

In either case, substituting (15) into (11) and simplifying gives equation for  $\gamma$

$$1 = (1 - \beta_f)[\lambda e^{-\gamma(Y - \alpha_f)} + (1 - \lambda) e^{\gamma \alpha_f}]. \quad (16)$$

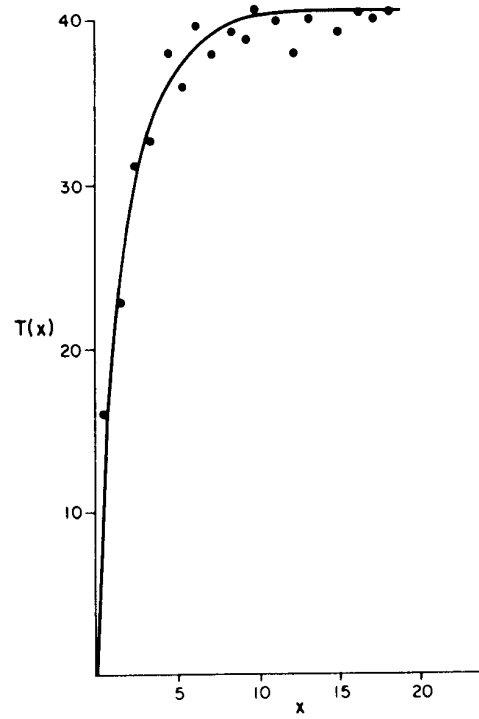
Since  $Y > \alpha_f$ , it is easily shown (16) has a solution  $\gamma > 0$ . The solution is found by an iterative scheme such as Newton's method without any difficulty.

In case *C*, once  $\gamma$  is known, the approximate behavior of the solution is known. For case *J*, the constant  $A$  is determined as follows. From (15),  $T(x_c) = (1 - A e^{-\gamma x_c})/\beta_f$ . Comparing this value with  $T(x_c)$  given by setting  $x = x_c$  in (11) gives an equation for  $A$ .

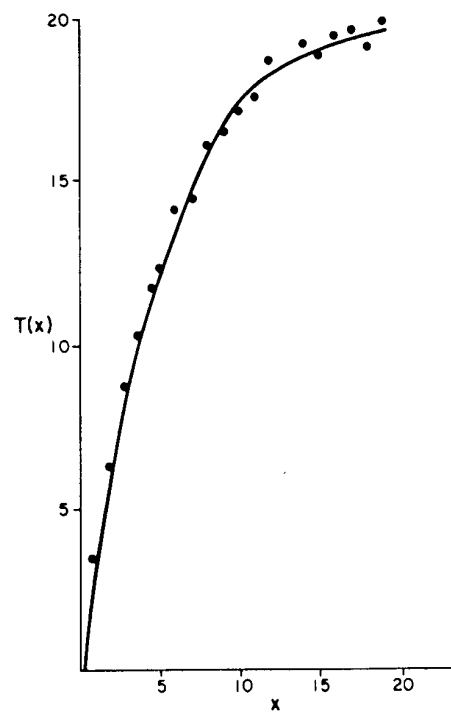
Figures 1–3 show a comparison of the theory (15)–(16) with stochastic simulations of the underlying process (using Eqs. (2) and (3)) for case *C*. The theory agrees remarkably well with the numerical experiments. (In the figures, the theoretical value was drawn continuously for ease of viewing.)

The theory given by (15) and (16) holds only for constant  $\lambda$  and  $\beta_f$ . It shows, however, how the general solution of (11) can be found. In order to do that, introduce a scaled variable  $z'$  defined so that

$$X(t) = Cz(t). \quad (17)$$



**Fig. 1.** Comparison of the asymptotic solution (—) with numerical simulations ( $\cdot$ ). Parameter values:  $Y=5$ ,  $\alpha_f=11$ ,  $\beta=0.025$ ,  $\lambda=0.4$ ,  $C=20$



**Fig. 2.** Comparison of the asymptotic solution (—) with numerical simulations ( $\cdot$ ). Parameter values:  $Y=5$ ,  $\alpha_f=1$ ,  $\beta=0.025$ ,  $\lambda=0.4$ ,  $C=20$

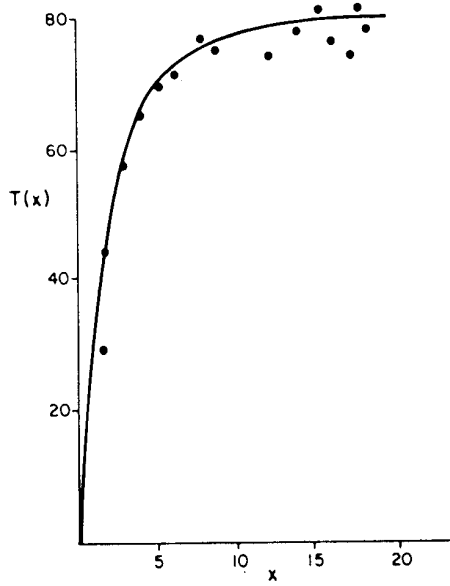


Fig. 3. Comparison of the asymptotic solution (—) with numerical simulations (·). Parameter values:  $Y = 5$ ,  $\alpha_f = 1$ ,  $\beta = 0.0125$ ,  $\lambda = 0.4$ ,  $C = 20$

The dynamics (2) are replaced by

$$z(t+1) = \min \left\{ 1, z(t) + \frac{1}{C} (\tilde{W}_i - \alpha_i(z)) \right\}. \quad (18)$$

It will be assumed that  $\varepsilon \equiv 1/C$  is a small parameter and that  $\varepsilon Y$  is less than 1 (i.e. that  $Y$  is not order  $1/\varepsilon$ ). Also, it helps to write (but is not essential) that

$$\begin{aligned} \lambda(x) &= 1 - \varepsilon \lambda_0(z) \\ \beta_f(x) &= \beta(z). \end{aligned} \quad (19)$$

Finally, define  $\tau(z)$  by

$$\tau(z) = T(x). \quad (20)$$

Using these in the general equation (11) gives

$$\tau(z) = 1 + (1 - \beta(z)) \{ (1 - \varepsilon \lambda_0(z)) \tau(z') + \varepsilon \lambda_0(z) \tau(z - \alpha_f \varepsilon) \} \quad (21)$$

where, in analogy with before,  $z' = \min\{1, z + \varepsilon(y - \alpha_f)\}$ . Rearranging (21) gives

$$\tau(z) = 1 + (1 - \beta(z)) \{ \tau(z') + \varepsilon \lambda_0(z) [\tau(z - \varepsilon \alpha_f) - \tau(z')] \}. \quad (22)$$

Now, large  $x$  corresponds to  $z \approx 1$ . If a regular perturbation expansion

$$\tau(z) = \sum_{j=0} \tau_j(z) \varepsilon^j \quad (23)$$

is substituted into (22), the order 1 term gives

$$\tau_0(z) = 1 + (1 - \beta(z)) \tau_0(z'). \quad (24)$$

For small  $\varepsilon$ ,  $z' \approx z$  and (24) has the solution

$$\tau_0(z) \sim \frac{1}{\beta(z)}. \quad (25)$$

Equation (25) provides the outer solution once again. The full asymptotic solution can be obtained by assuming that

$$\tau(z) \sim \tau_0(z)(1 - A e^{-\gamma(z)/\varepsilon}) \quad (26)$$

where the function  $\gamma(z)$  is to be determined, subject to the conditions that  $\gamma(0) = 0$ , and  $A = 1$  in case *C* and  $A < 1$  in case *J*.

Using (26) in (21), and writing  $\hat{\lambda}(z) = \lambda(x)$  gives, after some simplification (assuming also that  $\min\{1, z + \varepsilon(Y - \alpha)\}$  is  $z + \varepsilon(Y - \alpha)$ )

$$e^{-\gamma(z)/\varepsilon} = (1 - \beta(z))\{\hat{\lambda}(z) e^{-\gamma(z + \varepsilon(Y - \alpha_f))/\varepsilon} + (1 - \hat{\lambda}(z)) e^{-\gamma(z - \varepsilon\alpha_f)/\varepsilon}\}. \quad (27)$$

Taylor expanding around  $z$  and keeping terms order 1 gives an ordinary differential equation for  $\gamma(z)$ :

$$1 = (1 - \beta(z))\{\hat{\lambda}(z) e^{-\gamma'(z)(Y - \alpha_f)} + (1 - \hat{\lambda}(z)) e^{\gamma'(z)\alpha_f}\} \quad (28)$$

with the initial condition  $\gamma(0) = 0$ .

The solution of (28), when used in (26) gives a complete solution of the lifetime equation.

#### 4. Iterative solution of the DPE and the advantage of being smart

In this section, the full DPE (10) is solved by an iterative method. The method is extremely simple and the proof of convergence is a simple example of a contraction mapping theorem (so the reader is encouraged to try it out for him or herself). The iteration scheme is defined as follows. Specify a  $T^0(x)$  and then define

$$T^{k+1}(x) = \max[T^k(x - \alpha_h), 1 + (1 - \beta_f(x))\{\lambda(x)T^k(x') + (1 - \lambda(x))T^k(x - \alpha_f)\}]. \quad (29)$$

Although the initial function  $T^0(x)$  is not extremely important (that is, the method seems to converge in virtually all cases) a good choice for  $T^0(x)$  can be picked as follows. Let  $T_f(x)$  denote the solution constructed in the previous section for the case in which the forager always forages and let  $T_h(x)$  denote the lifetime if the forager always hides. Then

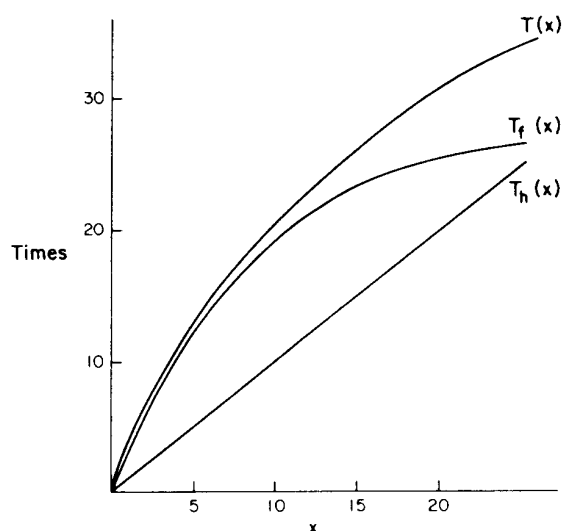
$$T_h(x) = \frac{x}{\alpha_h}. \quad (30)$$

The choice for  $T^0(x)$  is then

$$T^0(x) = \max(T_h(x), T_f(x)); \quad (31)$$

with this choice of  $T^0(x)$ , the iteration scheme (29) converges with great rapidity.

Figures 4 and 5 show  $T_h(x)$ ,  $T_f(x)$  and the iterative solution  $T(x)$ . The difference between either  $T_h(x)$  or  $T_f(x)$  and  $T(x)$  is a measure of the advantage of being smart (or behaving optimally). This difference is small when  $x$  is small, mainly because the forager must forage for small  $x$ . As  $x$  increases, the difference



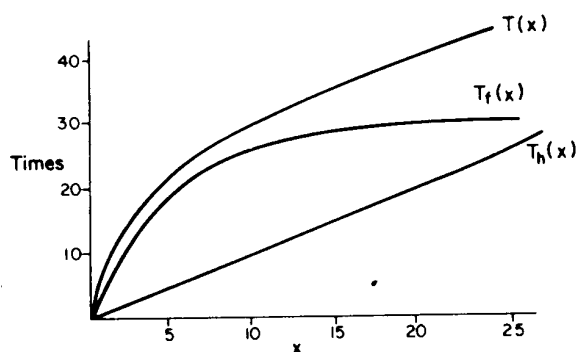
**Fig. 4.** Comparison of  $T(x)$ ,  $T_h(x)$  and  $T_f(x)$ . Parameter values:  $Y=3$ ,  $\alpha_f=2$ ,  $\alpha_h=1$ ,  $\beta=0.035$ ,  $\lambda=0.6$ ,  $C=25$

becomes much more impressive. For large  $x$ , there is considerable virtue in being smart.

### 5. Reproductive success of sit-and-wait predators

The methods developed in Sects. 2–4 of this paper can also be applied, with minor modifications, to the analysis of reproductive success for sit and wait predators such as spiders or some lizards. Consider the following model. Imagine a predator which waits for prey to arrive at its site. The probability that the  $i$ th prey type arrives between  $t$  and  $t+1$  is given by  $\lambda_i$ . If the predator chooses to attack this prey, it spends energy  $\alpha_i$  and kills the prey with probability  $\omega_i(x)$ . It may also be possible that while attacking a prey item, the predator itself may perish. Thus, let  $\beta_i(x)$  denote the probability that, given that the  $i$ th kind of prey is attacked, the predator is killed.

One can define reproductive success by assuming that once  $X(t)$  crosses a level of  $x_R$ , reproductive success occurs. For example, if  $X(t)$  is body weight,



**Fig. 5.** Comparison of  $T(x)$ ,  $T_h(x)$  and  $T_f(x)$ . Parameter values:  $Y=3$ ,  $\alpha_f=2$ ,  $\alpha_h=1$ ,  $\beta=0.035$ ,  $\lambda=0.7$ ,  $C=25$



then  $x_R$  could be the minimum weight needed for the production of a clutch of eggs. The maximum probability of reproductive success can then be defined by

$$u(x) = \max \text{Prob}\{X(t) \text{ crosses } x_R \text{ before } x_c \mid X(0) = x\}. \quad (32)$$

It is easily verified that  $u(x)$  satisfies the following functional difference equation

$$u(x) = (1 - \sum \lambda_i)u(x - \alpha_h) + \sum \lambda_i \max\{u(x - \alpha_h); \\ (1 - \beta_i)[\omega_i u(x'_i) + (1 - \omega_i)u(x - \alpha_i)]\} \quad (33)$$

where  $\alpha_h$  is now interpreted as the basal activity cost and  $x'_i = \min[x - \alpha_i + Y_i, C]$  where  $Y_i$  is the energetic value of the  $i$ th prey type. The boundary conditions associated with (33) are

$$\begin{aligned} u(x) &= 0 & x &\leq x_c, \\ u(x) &= 1 & x &\geq x_R. \end{aligned} \quad (34)$$

Equation (33) can be solved by exactly the same kind of iterative scheme as was used to solve the lifetime equation. Note that if one switches “max” to “min” in (32) and (33) and reverses the boundary conditions, then  $u(x)$  can be interpreted as the minimized probability of reproductive failure.

This kind of problem is often complicated by the requirement that reproduction occurs before some environmental event kills the predator. For example, funnel spiders in the desert need to produce an egg sac before the rainy season arrives. The arrival of the rains is a random event. Thus, let

$$\rho(t) = \text{Prob}\{\text{rainy season starts at the end of period } t\} \quad (35)$$

and define  $u(x, t)$  by

$$u(x, t) = \max \text{Prob}\{X(s) \text{ crosses } x_R \text{ before } x_c \\ \text{and before the rains arrive} \mid X(t) = x\}.$$

Assume that there is a  $T$  that  $\rho(T) = 1$ ; that is, that the rainy season surely starts at the end of period  $T$ . Then  $u(x, t)$  satisfies

$$\begin{aligned} u(x, t) &= 0 & x &\leq x_c \\ u(x, t) &= 1 & x &\geq x_r \\ u(x, T) &= \begin{cases} 0 & \text{if } x < x_r, \\ 1 & \text{if } x \geq x_r. \end{cases} \end{aligned} \quad (37)$$

The functional difference equation that  $u(x, t)$  satisfies is

$$u(x, t) = \{1 - \rho(t)\}[(1 - \sum \lambda_i)u(x - \alpha_h, t+1) + \sum \lambda_i \max\{u(x - \alpha_h, t+1); \\ + (1 - \beta_i)[\omega_i u(x'_i, t+1) + (1 - \omega_i)u(x - \alpha_i, t+1)]\}]. \quad (38)$$

This equation can be solved by time iteration, as in Mangel and Clark (1986), starting at  $t = T$  and working backwards. One can think of  $x = x_r$  as an “entrance boundary” from which probability flows into the region  $x < x_r$ . It’s also interesting to note that, in contrast with differential equations, for the foraging models time dependent problems are easier to solve than time independent ones. (One can be done exactly; the other only approximately). An interesting state of affairs, to be sure.

## 6. Discussion and conclusion

In this paper two methods were developed for the solution of the functional difference equations that arise in behavioral theory. The first is an asymptotic method for solving equations which do not involve an optimization step. This method is essentially an adaptation of the WKB method (Bender and Orszag (1978)) to the functional difference equations of behavioral theory. The second is an iterative, numerical method for the solution of the dynamic programming equation characterizing mean lifetime. Both methods have broader applicability than the equations discussed in this paper. For example, the WKB method can be used to analyze the behavior of the "Holling hungry mantid" in the spirit of Heijmans (1984). As already mentioned, the functional iteration scheme can be applied to models for decision making by a sit-and-wait predator. Both methods are easy to use and involve relatively modest computer requirements such as a good personal computer.

The methods developed in this paper can be applied to continuous time problems, too. In the continuous time formulation, the quantities defined in (1) are now viewed as rates (i.e. multiply each of the left-hand sides by  $dt$  to obtain probabilities). The equation that  $T(x)$  satisfies is now derived as follows. In analogy to (10), one has

$$T(x) = \max\{T(x - \alpha_n dt); dt + (1 - \beta_f(x) dt)\{\lambda dt T(\min(x - \alpha_f dt + Y, C)) + (1 - \lambda dt)T(x - \alpha_f dt)\}\}. \quad (39)$$

Taylor expanding in powers of  $dt$ , dividing by  $dt$  and letting  $dt$  approach 0 converts (39) into the following equation

$$0 = \max\{-\alpha_n T'(x); 1 + \lambda(x)T(\min(x + Y, C)) - \alpha_f T'(x) - (\beta_f(x) + \lambda(x))T(x)\}. \quad (40)$$

Equation (40) is a nonlinear, functional differential-difference equation. It can be solved by an extension of the methods developed in this paper (cf. Hanson and Tuckwell (1978) or Cope and Tuckwell (1979)).

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