

and the coefficient of variation is 100%), the expected reproduction in the period following sampling is nearly 40% higher than in expected reproduction in the period of sampling. This *value of information* is considerable, even though the parasitoid can only stay in the current patch or visit at most one more patch. A similar result is obtained if depletion is taken into account (Mangel and Clark, 1983).

Second (Mangel, 1990b), in a changing environment, there generally is an advantage (also see Stephens, 1991) to both updating parameters and to forgetting past information. A simple method for forgetting past information is to weight data collected  $p$  periods previously by  $e^{-mp}$  where  $m$  is a weighting parameter. When  $m = 0$ , all information collected is remembered but when  $m > 0$ , past information is forgotten at a rate which increases as  $m$  increases. The parameters for the probability density of  $\lambda$  are now functions  $v(S)$  and  $\alpha(S)$  of time spent in the patch, with  $v(0) = v_0$  and  $\alpha(0) = \alpha_0$ . The updating rule becomes (Mangel, 1990b)

$$v(S + 1) = e^{-m}v(S) + K + (1 - e^{-m})v_0$$

$$\alpha(S + 1) = e^{-m}\alpha(S) + 1 + (1 - e^{-m})\alpha_0$$

This is a "linear operator" (Kacelnik et al., 1987) of the form commonly used in psychological studies of learning.

In conclusion,

- There is a selective advantage, in terms of lifetime reproduction, in acquiring information about the world and using that information to shape behavior.
- The selective advantage of such learning is a broad function of the amount of effort put into sampling so that precise point optima are not expected.
- In an environment which is changing, there is a selective advantage to "forgetting" past information. The fitness value of forgetting is also a relatively flat function of the rate at which the past is forgotten. Thus, there will be selective pressures for both sampling the environment (learning) and forgetting past information.

### **Motivation: Behavioral Changes Induced by Egg Maturation**

In the previous section, experience (encounters with hosts) led to changes in behavior, without any concomitant change in physiological state. It may be, however, that changes in behavior occur solely because of changes in physiological state such as egg complement (Singer 1982, 1983, 1986; Singer et al., 1990). In such a case, we wish to develop a model in which behavior

changes with experience, but the description of the external environment does not change.

A synovigenic insect (one which matures eggs over time) encounters host type  $i$  with probability  $\lambda_i$  in a single period of time. Unlike the previous case, I assume that no updating of the values of the  $\lambda_i$  occurs during the search for oviposition sites. Assume that  $X(t)$  is the egg complement at time  $t$  and that when a host is accepted for oviposition, the entire current egg complement is laid (see Tatar, 1991; unpublished data). Laying a clutch of size  $x$  on a host of type  $i$  increases the mother's lifetime reproduction by  $f_i x$  where  $f_i$  characterizes the "quality" of the host, from the perspective of the larvae. For simplicity no larval density dependence is assumed; this can be modified (cf. Roitberg et al., 1990). Oviposition of  $x$  eggs requires handling time  $\tau(x) = \tau_0 + \tau_1 x$ , where  $\tau_0$  is a fixed time needed for oviposition (e.g., host recognition and handling) and  $\tau_1$  is the variable time required per egg. The probability of mortality during search is  $\mu_s$  and during oviposition is  $\mu_{op}$ .

Expected lifetime reproduction is defined by

$$F(x, t, T) = \text{maximum } E \{ \text{reproduction accumulated from} \\ \text{ovipositions between } t \text{ and } T \mid X(t) = x \} \quad (8)$$

For simplicity, assume that there are only two host types and that  $f_1 > f_2$  so that larval performance is superior on host type 1. Also assume that the time period is chosen so that the insect can mature one egg during each period and that the maximum egg complement is  $x_{\max}$ . Under the assumption that acceptance of a host leads to oviposition of the entire egg complement (cf. Mangel, 1987), the equation that  $F(x, t, T)$  satisfies is

$$\begin{aligned} F(x, t, T) = & (1 - \lambda_1 - \lambda_2)(1 - \mu_s)F(x', t + 1, T) \\ & + \sum_{i=1}^2 \lambda_i \max \{ f_i x + (1 - \mu_{op})^{\tau(x)} F(\tau(x), t + \tau(x), T); \\ & (1 - \mu_s)F(x', t + 1, T) \} \end{aligned} \quad (9)$$

The first term on the right-hand side of (9) corresponds to the event that no host is encountered during period  $t$ . Otherwise, a host of type 1 or type 2 is encountered. When a host is encountered, the insect's behavior involves acceptance (with increment in lifetime reproduction) or rejection of the host. The first term following the "max" corresponds to acceptance of the host. In this case, lifetime fitness is incremented by  $f_i x$ , the elapsed time for oviposition is  $\tau(x)$ , the entire egg complement is laid, and  $\tau(x)$  new eggs are matured during the process. The second term following the max