

Oviposition site selection and clutch size in insects

Marc Mangel

Departments of Agricultural Economics, Entomology and Mathematics*, University of California, Davis, CA 95616, USA

Abstract. Oviposition site selection and clutch size in parasitic insects can be viewed as problems in foraging theory. In this paper, a number of models for site selection and clutch size are developed, based on a dynamic state variable approach to optimal oviposition strategies. The models lead to predictions that are consistent with existing experimental data and suggest future experiments. Using these models shows the importance of constraints and state variables in the analysis of behavioral problems.

Key words: Oviposition behavior — Dynamic models — Foraging theory

Introduction

An ovipositing insect shares many of the same kinds of problems that animals foraging for food face: oviposition sites are often encountered randomly and may vary in quality and the future of the insect is inherently uncertain. One can thus view an insect's decision about where to lay eggs and how many eggs to lay as a problem in foraging theory (Charnov and Skinner (1984), (1985), Iwasa et al. (1984), Parker and Courtney (1984), Roitberg et al. (1982), Roitberg and Prokopy (1982), (1983), (1984), Skinner (1985)). The purpose of this paper is the development of a theory concerning oviposition behavior in parasitic insects. These are broadly defined to include insects that are parasites of other insects (e.g. parasitic wasps) and insects of economic importance that parasitize fruit (e.g. the Mediterranean fruit fly *Ceratitis capitata* Wied. or the apple maggot *Rhagoletis pomonella* Walsh). The behavioral theory developed in this paper is based on state variable models and Markov decision processes (Mangel and Clark (1986)). This paper is motivated by recent experimental studies on oviposition site selection and clutch size. These will be briefly reviewed before the mathematical theory is developed. The third section contains a description of the state variable approach to behavioral modelling and a family of models, developed by making differing assumptions about the biology of the parasitic insect. The fourth section contains the results of computer experiments. It will

* Address correspondence to Department of Mathematics

be seen that virtually all of the experimental results described in the next section can be understood by using state variable models and that new experiments are suggested by the theory. The fifth section contains a brief comparison with other theories and the sixth section contains a discussion of results and directions for future work. There are two appendices. The first shows the connection between the state variable models developed in this paper and usual life history theory. The second contains a discussion of oviposition behavior in a completely deterministic environment.

Experimental background

Recent analyses have determined the fitness female insects accrue by laying a clutch of C eggs in a host (Charnov and Skinner (1984), (1985), Skinner (1985), Waage and Godfray (1985), Weis et al. (1983)). The results of these analyses are that fitness is often a concave function of clutch size. Thus, one can determine that there is an "optimal" clutch that maximizes the fitness obtained from laying eggs on an individual host. In the rest of this paper, the singlet host optimum clutch will be called the "Lack Clutch Size" (LCS) or "Single Host Maximum" (SHM) in analogy to Lack's theory about clutch size in birds (Lack (1954)). The experiments also show, however, that insects often laid clutches which were far smaller than the single host optimum (Charnov and Skinner (1984), Weis et al. (1983)). For example, Table 1 shows the estimated frequency of clutch sizes for the parasitic wasp *Nasonia vitripennis*, based on data in Charnov and Skinner (1984). The SHM clutch size for single host optimum fitness are also shown in this table. The wasps laid clutches of virtually any size smaller than the SHM. Weis et al. (1983) report similar results.

Another series of experiments has focused on the foraging behavior of apple maggot and the response of the apple maggot to its oviposition marking pheromone (OMP). Roitberg and Prokopy (1983) found that after host deprivation, apple maggots were much more likely to oviposit in marked fruit than if

Table 1. Frequency of clutch sizes reported by Charnov and Skinner (1984)

Host volume	Clutch size				
	1-5	6-10	11-15	16-20	21-25
0-10	9	4	0	0	0
10-20	19	8	3	0	0
20-30	24	22	13	4	3
>30	11	18	15	6	6
Totals	63	52	31	10	9
Single host maximum (Lack) clutch sizes					
	Host volume		SHM clutch		
	18		11		
	22		15		
	31		21		

no host deprivation occurred. For example, a 5-min host deprivation period lead to 10% of the flies ovipositing in marked fruit, a 20–40-min deprivation period lead to 60% ovipositing, and an 80-min deprivation period lead to 85% ovipositing. Roitberg and Prokopy (1982) also report that flies spent about 25 times longer in patches of hawthorn fruit than is predicted by a marginal value argument. Roitberg et al. (1982) measured both the residence time (total time spent in a patch of fruit) and the giving up time (time since the last oviposition before the fly left the patch) for fruit patches of various sizes. They found that the residence time increased with the number of fruit in the patch and that the giving up time decreased.

Carey and Freeman (to appear) measured the response of medfly to artificial hosts of differing volumes. They found that the number of eggs laid per host saturates with host volume, ranging from 2 eggs per clutch for hosts of 1.5 cm diameter to 3–4 eggs per clutch for hosts larger than 3 cm in diameter. Since the medfly can easily lay 60 eggs per day, it is unlikely that this saturation is caused by egg depletion. Medflies also respond to host deprivation by delaying the onset of senescence (cf. Williams (1957)) and increasing egg production at later ages (Carey et al. (1986)).

Godfray (1986) studied clutch size in a leaf-mining fly (*Pegomya nigrirarsis*: Anthomyiidae) and found that the predicted optimal clutch size (3) was indeed the most frequently observed clutch size. This observation seems at first to be at odds with the observation of Charnov and Skinner, but it will be seen that through a proper theoretical development one can understand the differences in these observations. Jaenike (1978) quotes a study by Wiklund (1977) of the butterfly *Leptidea sinapis* that shows the need for simultaneously considering predation and oviposition in a model of behavior. Jaenike writes: “Perhaps these butterflies confine their feeding to the wood because of the possibility of predation in the meadow. If this were the case then forays into the meadow to oviposit on *L. pratensis* would incur a potential risk, making *L. montanus* a more acceptable host plant”.

Although not concerned with insects, Browne’s (1982) work on the brine shrimp *Artemia* is especially noteworthy because it examines the interaction between nutritional state and reproductive success and shows the need for a theory that connects physiological state and reproductive behavior. Fritz and Morse (1985), Loschiavo (1964) and Snell and King (1977) report similar data, but without reference to theory.

Even though theory for the oviposition behavior of parasitic insects is already extensive (Carey (1984), Charnov and Skinner (1984), (1985), Houston and McNamara (1986), Iwasa et al. (1984), Jaenike (1978), Parker and Courtney (1984), Price (1977), Skinner (1986) and Williams (1957)), the preceding experimental results point out at least five key questions that are not completely resolved: (1) why is there a distribution in observed clutch sizes and in particular why should the observed clutch sizes be much smaller than the single host optimum clutch; (2) what is the explanation of the response to host deprivation; (3) why does clutch size saturate with host volume; (4) how are nutritional state and reproductive behavior connected; and (5) how does one assess trade-off between the risk of mortality and the chance of reproductive success? The behavioral

theory developed in this paper provides a means for attacking these questions and for developing future experiments. It is worth noting that the main issue of this paper, reproductive trade-offs, is much broader than parasitic insects (Pianka (1976)) so that many of the ideas developed here have the potential for wider applicability.

State variable models in behavioral theory

In this section, Markovian decision theory (e.g. Aoki (1967), Heyman and Sobel (1984) or Mangel (1985)) is used to develop a framework in which insect oviposition behavior can be analyzed. The theory requires three main components: (1) a state variable or variables (characterizing the current state of the insect) and its dynamics, (2) a survival function relating current state and behavior to survival in the future, and (3) a measure of fitness, which represents the quantity that is being maximized.

For most of the work reported in this paper, a discrete time formulation will be used and $X(t)$ will denote the value of the state variable at the start of period t . For the particular problem of host site selection and clutch size, three possible choices for the state variable are:

- the number of mature eggs held by an insect at the start of period t ,
- the number of oocytes (“potential eggs” or “egg seeds” (Fletcher and Comins (1985))) at the start of period t , or
- a measure of energetic reserves at the start of period t .

In general, one can use various combinations of these three state variables to model different kinds of insects and different environmental situations. The particulars of the model depend, to some extent, on the particular problem being considered. The dynamics of $X(t)$ also depend upon the choice of state variable.

Survival is defined by a function $\mu(x, t, d)$ as follows:

$$\mu(x, t, d) = \text{Prob}\{\text{insect is alive at the start of period } t+1 \mid \text{alive at the start of period } t, X(t) = x \text{ and the behavioral decision during period } t \text{ is } d\}. \quad (1)$$

Note that $X(t)$ can be interpreted as a vector or scalar in this equation. If one were to assume that $\mu(x, t, d)$ were a function only of time, then $\mu(t)$ could be calculated from the standard l_t schedule of demographic theory (see, e.g. Carey (1982) for an application of demographic theory to medfly). In particular, since l_t is the probability of surviving to the start of period t , one has

$$\begin{aligned} \mu(t) &= \text{Prob}\{\text{survival to period } t+1 \mid \text{alive a period } t\} \\ &= \text{Prob}\{\text{survival to } t+1\} / \text{Prob}\{\text{survival to } t\} \\ &= l_{t+1} / l_t. \end{aligned} \quad (2)$$

Alternately, one could measure survival only in terms of the state variable (see, e.g. Iwasa et al. (1984)) in which case $\mu = \mu(x)$ can be interpreted as a survival function measured in “physiological time”. In general, one needs to assume that survival depends upon both time and the state variable (and possibly the

behavioral decision) in order to understand the experimental results that were described previously.

When an insect encounters a potential host, it must decide (1) whether or not to oviposit in that host and (2) how many eggs to lay if the decision is to oviposit. Assume that a clutch of size c laid in a host of type i when the current value of the state variable is $X(t) = x$ gives an increment in fitness F proportional to

$$\delta F = W_i(c, x, t) \quad (3)$$

in which the function $W_i(c, x, t)$ is computed in a manner analogously to the computations described by Charnov and Skinner (1984), (1985), Skinner (1985) or Weis et al. (1983). In many cases, it is reasonable to assume that

$$\delta F = W_i(c)h_i(x, t) \quad (4)$$

where $W_i(c)$ is the fitness of a clutch of size c conditioned on perfect survival and $h_i(x, t)$ is the fraction of eggs that hatch on a host of type i when $X(t) = x$. Carey (1984) provides data that can be used to estimate the hatch function. In some cases, the fitness increment might also be a function of the time remaining in the current season. That is, if T denotes the time at which the season ends (e.g. the first frost arrives), then $\delta F = W_i(c, x, t, T)$. This situation would arise in a growing population with more than one generation per year, so that offspring which are produced early in the season have more value than offspring produced later in the season. For most of this paper, the T dependence of the fitness increment will be suppressed. One can think either of a univoltine insect or of a population at equilibrium.

It is reasonable to assume that $W_i(0) = 0$ and that there exists a clutch size $c_m(i)$ that provides a maximum value of fitness through oviposition on a host of type i . Two useful conceptual models for the fitness increment are $W_i(c) = r_i c(1 - c/K_i)$ (a "logistic" fitness increment) and $W_i(c) = a_i c \exp(-b_i c)$ (a "Ricker" fitness increment). The value $c_m(i)$ thus corresponds to the single host optimum clutch size or the Lack clutch size.

An insect making the decision concerning oviposition and clutch size, given that a host of a certain type has been encountered, thus faces a trade-off between an immediate increment in fitness from oviposition on the current host and the loss of future expected fitness caused by oviposition on the current host and concomitant changes in state variables and possibly survival functions. This trade-off can be dealt with in a unified and consistent manner by the method of stochastic dynamic programming (SDP). In order to show how this is done, a number of different state variable models will now be developed in detail. All of the models share the following assumptions:

- (1) There are H different host types, labelled by $i = 1, 2, \dots, H$. The incremental fitness function for a clutch of size c on a host of type i is $W_i(c)$. The probability of encountering a host of type i during period t is denoted by $\lambda_i(t)$.
- (2) There is a maximum time T after which no more fitness can be accrued to the insect. This time can be either the time of death or diapause of the insect or a time at which the hatch percentage is essentially 0.

Now define an expected lifetime fitness function $F(x, t, T)$ as follows:

$$F(x, t, T) = \text{maximum expected lifetime fitness through oviposition between } t \text{ and } T, \text{ given that } X(t) = x. \quad (5)$$

In light of the second assumption, $F(x, t, T)$ immediately satisfies the end condition that

$$F(x, T, T) = 0. \quad (6)$$

The values of $F(x, t, T)$ for $t \leq T - 1$, and the corresponding oviposition decisions, are obtained by solving the appropriate stochastic dynamic programming equations (DPEs) that characterize $F(x, t, T)$.

Model 1: Mature eggs only

The simplest model is one in which insects are born with all of their eggs already mature. This kind of model would apply to Lepidoptera in general, some Diptera, and some Coleoptera, so that as a starting point it is not totally devoid of realism. Let $X(t)$ denote the number of eggs which remain at time t . Then $X(0) = R$, where R is the initial reserve of eggs, and $X(t+1)$ is related to $X(t)$ by the simple difference formula

$$X(t+1) = X(t) - C(t) \quad (7)$$

where $C(t)$ is the clutch laid in period t . If $C(t) = 0$, which would occur if the insect chooses an activity other than ovipositing or doesn't find a suitable host, then $X(t+1) = X(t)$. Otherwise $X(t+1) < X(t)$. It is clear too that $X(t) \geq 0$ is a constraint on the state variable (in this model only — see below for variations) for all values of t .

The DPE for $F(x, t, T)$ is computed in the following way. If a host of type i is encountered in period t and a clutch of size c is laid, then two events occur. The first is that an increment in fitness $W_i(c, x, t)$ is added to the total expected lifetime fitness of the insect. The second is that if the insect survives to the start of period $t+1$, then the value of the state variable at the start of period $t+1$ is $x - c$. The total expected lifetime fitness of an insect starting at period t with $X(t) = x$ is then the sum of the increment $W_i(c, x, t)$ and the expected lifetime fitness from period $t+1$ on, conditioned on survival. The maximum expected lifetime fitness is obtained by maximizing over the clutch size decision. Thus

$$F(x, t, T) = \sum \lambda_i \max_{0 \leq c \leq x} \{ W_i(c, x, t) + p(x, c, t) F(x - c, t + 1, T) \}. \quad (8)$$

The sum on the right-hand side of (8) goes over all host types; the terms are respectively the probability of finding a host of type i , the action of maximizing over clutch size subject to the constraint that the clutch must be smaller than the number of eggs that remains, the increment to lifetime fitness from the clutch of size c in period t , and the expected fitness starting at period $t+1$. Note that $c = 0$ is a perfectly legitimate decision and means that no eggs are used in period t if a host of type i is encountered.

In order to analyze the dynamic programming equation (8), begin by setting $t = T - 1$ so that one is interested in the next to the last period. In this case, Eq. (8) becomes

$$F(x, T - 1, T) = \sum \lambda_i \max_{0 \leq c \leq x} W_i(c, x, T - 1) \quad (9)$$

and Eq. (9) immediately leads to two predictions:

- P_1 : Older insects should be less selective about where they lay their eggs. For example, there should be more superparasitism (in which insects oviposit in hosts that were already parasitized) as the insects near death.
- P_2 : Imagine a cohort of identical insects that start life together. By period $T - 1$, random encounters with hosts of different types will lead to a varying number of eggs remaining per insect and thus to the prediction that there will be a distribution in clutch sizes, since the constraint $c \leq x$ has a potentially different value for each insect. Conversely, in a laboratory situation in which the host encounters of differing insects can be carefully controlled, one would predict less variation in clutch size.

Although these predictions appear to be "obvious", it is in fact the formulation of the problem in terms of a dynamic state variable that makes them so obvious. Further understanding of oviposition decision making requires solution of the dynamic programming equation.

Equation (8) is easily and quickly solved on a desktop microcomputer once the fitnesses and survival functions are specified. For the results presented here, the incremental fitnesses $W_i(c, x, t)$ were treated as functions only of host type and clutch size, so that the incremental fitness is denoted by $W_i(c)$. The fitnesses were modelled using the data shown in Fig. 7 of Charnov and Skinner (1984). The curves were extended more or less symmetrically and then fit with a cubic of the form $W_i(c) = A_0(i) + A_1(i)c + A_2(i)c^2 + A_3(i)c^3$. Table 2 shows the values of the coefficients and the SHM clutch. (Although the cubic form for $W_i(c)$ treats c as a continuous variable, only discrete values of c are allowed when solving the dynamic programming equation). Most of the calculations reported here used an initial reserve of $R = 125$ eggs and a foraging time horizon $T = 20$ periods. The host encounter rates are treated as exogenous parameters that are constant over time and the survival probability is treated as a function of time only, using one of two l_t schedules:

$$l_t = \begin{cases} 1 \text{ up to period } T - 1 \text{ and } 0 \text{ in period } T & \text{(a)} \\ 1 - (t^\gamma / T^\gamma) & \text{(b)} \end{cases} \quad (10)$$

When the DPE (8) is solved, the first output is the expected lifetime fitness function $F(x, t, T)$ from period t onwards. One finds that $F(x, t, T)$ is a non-decreasing function of both the initial egg complement x and the time to go $T - t$. These results are easily understood and intuitive: as either the number of periods remaining or the initial number of eggs increases, the expected lifetime fitness should either increase or level off (if there is insufficient foraging time to oviposit the entire complement of eggs).

A second and more interesting output of the dynamic programming equation is the optimal oviposition decision. That is, when solving the DPE one finds the

Table 2. Coefficients used in the fitness function $W_i(c) = A_0 + A_1c + A_2c^2 + A_3c^3$ (valid for $c \leq 30$)

Host type	A_0	A_1	A_2	A_3	SHM clutch
1	-0.2302	2.7021	-0.2044	0.0039	9
2	-0.1444	2.2997	-0.1170	0.0013	12
3	-0.1048	2.2097	-0.0878	0.0004222	14
4	-0.0524	2.0394	-0.0339	-0.0003111	23

optimal clutch $c^*(x, t, T; i)$ when a host of type i is encountered during period t with $X(t) = x$ and $T - t$ periods remaining. This quantity is more interesting than the fitness function itself since the optimal oviposition decision corresponds to the behavioral observations that one will make in experimental work. For example, Table 3 shows optimal oviposition decisions for a variety of parameter values. For short time horizons, the optimal clutch decision is the single host maximum or “Lack” clutch size. As the number of periods available for oviposition increases, the optimal clutch for a given host type decreases. These results suggest that clutches smaller than the SHM will be observed in nature; exactly this kind of result was reported by Charnov and Skinner (1984). One can understand the shift towards smaller clutches as the interplay of a concave fitness function, the time horizon and a survivorship function. Given a sufficiently long time horizon an insect with a concave fitness function should deposit as few eggs per host as possible since that will maximize the total lifetime fitness. It is only when the time horizon is short (so that eggs would remain at period T) or the future is uncertain (so that there is a considerable probability of death during a period) that one would expect clutches approaching the SHM clutch. It is shown in Appendix B that this reasoning is true even in a completely deterministic setting.

Generalizing the computational results leads to two more predictions:

- P_3 : Consider a host for which the SHM clutch is large. As the probability of finding this host increases, the observed distribution of clutches in this host will change so that small clutches are more frequent. Conversely, if encountering this host is a rare event, then the clutches in this host should be close to the SHM clutch.
- P_4 : Note from Eq. (8) that the survival $\phi(x, c, t)$ essentially “discounts” the value of future clutches. Thus, as the probability of mortality between periods increases, one should observe larger clutches more frequently.

These four predictions already provide insight into the experimental results. There is some overlap between these results and the work of Weis et al. (1983), who use demographic models, and Waage and Godfray (1985), but neither of those papers explicitly deal with the distribution of clutches. Such distributions are an immediate prediction of the state variable models.

Model 2: Unlimited eggs with conversion from energy to eggs

In this model, one assumes that the number of oocytes is essentially unlimited (not an unreasonable assumption in some cases—see Dunlap-Pianka et al.

Table 3. Optimal oviposition decisions

Time to go ($T - t$)	Optimal oviposition decision ^a			
	Host type 2		Host type 4	
	$x = 40$	$x = 80$	$x = 40$	$x = 80$
1	12	12	23	23
2	12	12	20	23
3	9	12	14	23
4	6	12	11	21
5	5	10	9	17
6	4	8	8	15
7	4	7	6	13
8	3	6	6	11
9	3	5	5	10
10	3	5	5	9
11	2	4	4	8
12	2	4	4	8
13	2	4	4	7
14	2	3	3	6
15	2	3	3	6
16	2	3	3	6
17	2	3	3	5
18	2	3	3	5
19	2	3	3	5
20	2	3	2	5

^aSurvival function given by Eq. (10a) and $\lambda_1 = 0.05$, $\lambda_2 = 0.05$, $\lambda_3 = 0.1$, $\lambda_4 = 0.8$

(1977)) and that the insect must expend energetic reserves converting oocytes to mature eggs. Since the number of oocytes is assumed to be unlimited, there is only one state variable. Let $X(t)$ denote the energy reserves of the insect at the start of period t . The insect faces two behavioral choices during period t ; these choices determine the dynamics of $X(t)$. If the choice is to forage for food during period t , then

$$X(t+1) = X(t) - \alpha_f(t) + Y(t) \quad (11)$$

where α_f is the cost of foraging during period t measured in terms of energetic reserves and $Y(t)$ is the (possibly random) energetic content of the food found during period t . It is reasonable to assume that in addition to the constraint that $X(t) \geq 0$, there is a minimum energy level x_m so that if $X(t)$ ever falls below this critical level the insect is dead. It is also possible to add other constraints to the dynamics without any difficulty. For example, if there is a capacity constraint, so that $X(t)$ can never exceed some capacity C , then the right-hand side of (11) is replaced by $\min(C, X(t) - \alpha_f(t) + Y(t))$. If there is a rate constraint, so that the per-period increment in the energetic reserves cannot exceed a value R , then the right-hand side of (11) is replaced by $X(t) + \min(R, Y(t) - \alpha_f(t))$.

If the behavioral decision during period t is to search for oviposition sites, then the dynamics of $X(t)$ are given by

$$X(t+1) = X(t) - \alpha_0(t) - \alpha_e C(t) \quad (12)$$

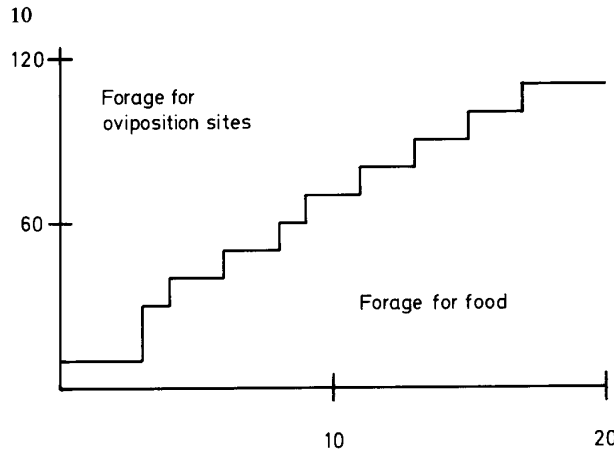


Fig. 1. Division of the state variable/time horizon plane into regions of foraging for food and for oviposition sites. Parameter values: $\gamma = 0.5$, $\lambda_1 = 0.25$, $\lambda_2 = 0.2$, $\lambda_3 = 0.15$, $\lambda_4 = 0.15$, $\alpha_f = \alpha_0 = 5$, $\alpha_e = 5$, $Y = 25$, $C = 125$

where α_0 is the energetic cost of searching for oviposition sites during period t , α_e is the energetic cost of converting one oocyte to a mature egg and $C(t)$ is the size of the clutch laid during period t ; in particular $C(t) = 0$ is a possibility.

Let $\lambda_f(t)$ be the probability of finding food during period t . Dropping the time dependence of the λ 's, the DPE for $F(x, t, T)$ is thus

$$F(x, t, T) = \max[\lambda_f F(x', t+1, T) + (1 - \lambda_f) F(x - \alpha_f, t+1, T); \sum \lambda_i \max_{0 \leq c \leq (x - \alpha_0)/\alpha_e} \{W_i(x, c, t) + \mu(x, c, t) F(x - \alpha_0 - \alpha_e c, t+1, T)\}] \quad (13)$$

where $x' = x - \alpha_f(t) + Y$, subject to any appropriate constraints. The first two terms on the right-hand side of Eq. (13) give the expected future lifetime fitness if the insect chooses to forage for food; the second two terms give the expected increment fitness and expected future lifetime fitness if the insect chooses to forage for an oviposition site. The decision rule is then to choose the action that contributes most to expected lifetime fitness.

The most interesting use of a model such as this one is the ability to be able to predict when the insect should forage for food and when it should forage for oviposition sites. Figure 1 shows a typical result from this model. The plane defined by "time to go/state variable" is broken into two regions. In one of the regions, the insect should forage for food and in the other it should forage for oviposition sites. (The step-like nature of the boundary is more or less an artifact of the model in which only one food value Y occurs. If there is a distribution of food values, then the boundary is a smoother curve.) Study of Fig. 1 suggests the following prediction:

P_5 : Insects will spend less time foraging for food and more time foraging for oviposition sites as they get older.

Model 3: Mature eggs and oocytes

In this model, it is assumed that the insect is born with a limited number Y_0 of oocytes which can be converted to mature eggs. Fletcher and Comins (1985), in

a model of the life history of *Dacus oleae*, refer to the oocytes as potential eggs. Let $X(t)$ denote the number of mature eggs held at the start of period t , $Y(t)$ denote the number of oocytes which remain at the start of period t and $r(x, y, t)$ denote the number of oocytes that can be converted to mature eggs during period t when $X(t) = x$ and $Y(t) = y$. The production function $r(x, y, t)$ should satisfy a number of reasonable conditions. For example, $r(x, 0, t)$ is certainly 0 and if there is a maximum capacity C of the number of mature eggs that can be held, $r(C, y, t)$ is also 0. The coupled dynamics of $X(t)$ and $Y(t)$ are then

$$\begin{aligned} X(t+1) &= X(t) - C(t) + r(X(t), Y(t), t) \\ Y(t+1) &= Y(t) - r(X(t), Y(t), t). \end{aligned} \quad (14)$$

The DPE for this particular case is derived and studied in detail in Mangel (1987), where the theory is applied to study the behavior of the rose hips fly *Rhagoletis basiola*.

Model 4: Energy, mature eggs and oocytes

Models 2 and 3 can be combined in what should by now be a relatively clear way so that one can consider expected lifetime fitness that depends upon energetic or nutrient reserves $E(t)$ at the start of period t , the number of mature eggs $X(t)$ held at the start of period t , and the number of oocytes $Y(t)$ remaining at the start of period t . The lifetime expected fitness function is now

$$\begin{aligned} F(e, x, y, t, T) &= \text{maximum expected lifetime fitness through egg} \\ &\quad \text{production between } t \text{ and } T, \\ &\quad \text{given that } E(t) = e, X(t) = x, \text{ and } Y(t) = y. \end{aligned} \quad (15)$$

The DPE for $F(e, x, y, t, T)$ should be clear to the reader; the main difficulty (if there is one at all) will be computational complexity.

Model 5: Mature eggs in continuous time

The four models discussed thus far deal with events in discrete time and this on occasion may cause difficulties for the interpretation of experimental results. Thus, one continuous time model will be developed, for the case in which the state variable $X(t)$ represents the number of mature eggs remaining at time t . (Note the shift in interpretation of the state variable if one works in continuous time. This is also true for the interpretation of the expected lifetime fitness function $F(x, t, T)$ which now is the expected lifetime fitness obtained by foraging for host sites between time t and T , given that $X(t) = x$.) Other variables are also changed accordingly:

$$\text{Prob}\{\text{encountering a host of type } i \text{ during the interval } (t, t + \Delta t)\} = \lambda_i \Delta t + o(\Delta t) \quad (16)$$

and

$$\begin{aligned} & \text{Prob}\{\text{an insect that is alive at time } t \text{ survives to time } t + \Delta t \mid X(t) = x, \\ & \quad \text{clutch of size } c \text{ is laid at time } t\} \\ & = 1 - \mu(x, c, t)\Delta t + o(\Delta t). \end{aligned} \quad (17)$$

(Especially note the change in the interpretation of the survivorship function.) In these equations, $o(z)$ denotes terms such that $o(z)/z$ approach 0 as z approaches 0.

The DPE for expected lifetime fitness is now derived as follows. One compares $F(x, t, T)$ and $F(x, t + \Delta t, T)$:

$$\begin{aligned} F(x, t, T) &= \sum \lambda_i \Delta t \max_{0 \leq c \leq x} \{ W_i(c, x, t) + (1 - \mu(x, c, t)\Delta t)F(x - c, t + \Delta t, T) \} \\ &+ (1 - \sum \lambda_i \Delta t)(1 - \mu(x, 0, t)\Delta t)F(x, t + \Delta t, T) + o(\Delta t). \end{aligned} \quad (18)$$

The right-hand side of Eq. (18) is now Taylor expanded in powers of Δt (see Mangel (1985) for a further description of this method for deriving dynamic programming equations) to give

$$\begin{aligned} F(x, t, T) &= \sum \lambda_i \Delta t \max_{0 \leq c \leq x} \{ W_i(c, x, t) + F(x - c, t, T) + o(\Delta t^2) \} \\ &+ F(x, t, T) + \partial_t F \Delta t - (\mu(x, 0, t) + \sum \lambda_i) \Delta t F(x, t, T) + o(\Delta t^2). \end{aligned} \quad (19)$$

Dividing by Δt and letting Δt approach 0 gives the equation

$$\partial_t F = \sum \lambda_i \max_{c \leq x} \{ W_i(c, x, t) + F(x - c, t, T) \} - (\mu(x, 0, t) + \sum \lambda_i) F(x, t, T). \quad (20)$$

This is a nonlinear, partial differential-difference equation. It still satisfies the end condition $F(x, T, T) = 0$ and still should be solved by some kind of backwards iteration. It is very likely that the solution methodology for dealing with Eq. (23) will involve the discretization of the equation over either time or state variables. The complexities and approximations associated with such a discretization, however, make the continuous time model no more compelling than the much simpler discrete time models.

Model 6: Mature eggs and variable handling times

There are many situations in which host types are sufficiently varied that one needs to consider handling times that are functions of host type and clutch size. Thus, one would define $\tau_i(c)$ as the time needed to lay a clutch of size c in a host of type i . The biology of the insect-host system must determine the form of the variable handling time, and the way that fitness is accrued to the insect. At least two broad cases can be envisioned: (i) the entire clutch is laid at once and there is no gain in fitness for the insect until the handling time elapses; (ii) the handling time for a clutch of size c is the sum of handling times for the first egg, second egg, etc. up to the c th egg and the fitness is increased incrementally. In either case, however, it is no longer sufficient to describe the state of the insect by the value of $X(t)$ only. One must include the activity of the insect at the start

of period t (searching for a host site or ovipositing) and, if the activity is ovipositing, how long the insect has spent on the current host. Thus define the following fitness functions:

$$F(x, t, T) = \text{maximum expected fitness between } t \text{ and } T, \text{ given that } X(t) = x \text{ and the insect is searching at the start of period } t \quad (21)$$

$$F_{il}(x, s, t, T) = \text{maximum expected fitness between } t \text{ and } T, \text{ given that } X(t) = x, \text{ the insect will lay a clutch of size } l \text{ on a host of type } i, \text{ and the insect has already spent } s \text{ units of time on the host.}$$

Assuming the first case, in which fitness is accrued only at the end of the handling time, the DPEs are

$$F(x, t, T) = \sum \lambda_i \max \left\{ \mu_s F(x, t, t+1, T); \max_c \mu_i(x, c, t) F_{ic}(x, 1, t, T) \right\} \quad (22a)$$

and

$$F_{ic}(x, s, t, T) = \begin{cases} W_i(c) + F(x - c, t+1, T) & \text{if } s = \tau_i(c) - 1 \\ F_{ic}(x, s+1, t+1, T) & \text{otherwise} \end{cases} \quad (23b)$$

where now μ_s and $\mu_i(x, c, t)$ are respectively the probability of surviving one period while searching for a host and the probability of surviving through the handling time $\tau_i(c)$ on a host of type i while ovipositing.

Experiments with computer insects

One can use Monte Carlo simulation to perform experiments on “computer insects”. These model insects are assumed to behave optimally according to the dynamic state variable models and encounter hosts randomly (the Monte Carlo method is used to simulate the encounters with hosts). In the simulations reported here, model 1 was used. In each simulation, 100 computer insects were allowed to forage for host sites for 20 periods. Each insect started with 120 mature eggs and, upon encountering a host, determined the optimal oviposition behavior based on the solution to the DPE. Table 4 shows the various “experimental” set-ups used for the computations.

Experiment 1: Effect of host distribution

The effects of the distribution of hosts on the oviposition behavior of the insects can be studied by varying the encounter probabilities $\lambda_1 - \lambda_4$. The effects of host distribution on the distribution of clutches is shown in Table 5. Note that a higher probability of encounter with the hosts for which the single host optimum clutch is large leads to a smaller frequency of large clutches. This can be interpreted as a “risk spreading mechanism”, although the optimal decision does not in any way model the risk trade-offs directly. That is, when large hosts are plentiful the concavity of the fitness increments means that it is advantageous for the insect to deposit fewer eggs per host, since the likelihood of encountering another large host is high. Second, note the interplay of probability of survival and clutch

Table 4. Parameter values used in different cases for the computer experiments

Case	T	λ_1	λ_2	λ_3	λ_4	Survival function
1	20	0.1	0.1	0.1	0.1	10a
2	20	0.05	0.05	0.1	0.8	10a
3	15	0.1	0.1	0.1	0.1	10a
4	15	0.05	0.05	0.1	0.8	10a
5	10	0.1	0.1	0.1	0.1	10a
6	10	0.05	0.05	0.1	0.8	10a
7	20	0.1	0.1	0.1	0.1	10b, $\gamma = 1$
8	20	0.05	0.05	0.1	0.8	10b, $\gamma = 1$
9	15	0.1	0.1	0.1	0.1	10b, $\gamma = 1$
10	15	0.05	0.05	0.1	0.8	10b, $\gamma = 1$
11	10	0.1	0.1	0.1	0.1	10b, $\gamma = 1$
12	10	0.05	0.05	0.1	0.8	10b, $\gamma = 1$
13	20	0.1	0.1	0.1	0.1	10b, $\gamma = 2$
14	20	0.05	0.05	0.1	0.8	10b, $\gamma = 2$
15	15	0.1	0.1	0.1	0.1	10b, $\gamma = 2$
16	15	0.05	0.05	0.1	0.8	10b, $\gamma = 2$
17	10	0.1	0.1	0.1	0.1	10b, $\gamma = 2$
18	10	0.05	0.05	0.1	0.8	10b, $\gamma = 2$

size. The overall distribution of clutch sizes is thus caused by the interplay of the stochastic environment and the state variable dynamics. The results of this computer experiment show the same kinds of trends as the experimental results of Charnov and Skinner (1984).

Experiment 2: Effects of host deprivation

In terms of a dynamic state variable model, host deprivation is equivalent to a reduction in the time available for foraging for oviposition sites. For the models developed in this paper, in which encounter probabilities are constant, one can think of host deprivation as a reduction in the final time T . Table 6 shows the

Table 5. Results of the host distribution experiment^a (entries are frequency of observed clutches)

Case	Clutch size					
	1-5	6-10	11-15	16-20	21-25	>25
1	0.02	0.35	0.41	0.15	0.07	
2	0.24	0.76	0	0	0	
7	0.01	0.26	0.52	0.04	0.17	
8	0.14	0.29	0.57	0	0	
13	0.013	0.271	0.510	0.054	0.152	
14	0.16	0.36	0.48	0	0	

^a Cases 1, 7 and 13 correspond to all $\lambda_i = 0.1$. Cases 2, 8, and 14 correspond to $\lambda_1 = \lambda_2 = 0.05$, $\lambda_3 = 0.1$, $\lambda_4 = 0.8$. In all cases, $T = 20$. The survival function is Eq. (10a) for cases 1, 2; (10b) with $\gamma = 1$ for cases 7, 8 and (10b) with $\gamma = 2$ for cases 13, 14

Table 6. Results of the host deprivation experiment (entries are the frequencies of observed clutches)

Case	T	Clutch size				
		1-5	6-10	11-15	16-20	21-25
1	20	0.02	0.35	0.41	0.15	0.07
3	15	0.008	0.301	0.459	0.046	0.186
5	10	0	0.260	0.481	0.003	0.256
2	20	0.24	0.76	0	0	0
4	15	0.163	0.821	0.016	0	0
6	10	0.023	0.210	0.742	0.023	0.002
7	20	0.01	0.26	0.52	0.04	0.17
9	15	0.004	0.249	0.495	0.007	0.245
11	10	0	0.233	0.505	0	0.262
8	20	0.14	0.29	0.57	0	0
10	15	0.082	0.278	0.325	0.315	0
12	10	0.029	0.178	0.137	0.656	0
13	20	0.013	0.271	0.510	0.054	0.152
15	15	0.003	0.236	0.485	0.023	0.253
17	10	0	0.242	0.512	0	0.246
14	20	0.16	0.36	0.48	0	0
16	15	0.11	0.27	0.62	0	0
18	10	0.04	0.19	0.18	0.59	0

^a Cases 1-6 have survival function Eq. (10a). Cases 7-12 have survival function Eq. (10b), with $\gamma = 1$. Cases 13-18 have survival function Eq. (10b) with $\gamma = 2$

For odd numbered cases, all $\lambda_i = 0.1$; for even numbered cases $\lambda_1 = \lambda_2 = 0.05$, $\lambda_3 = 0.1$ and $\lambda_4 = 0.8$

results of a host deprivation computer experiment. Shorter time horizons lead to a clutch size distribution that is skewed more towards larger clutches, although there is still considerable variation in the size of clutches. Mangel (1987) does a similar kind of computer experiment in attempting to understand the oviposition behavior of Tephritid fruit flies, in particular *Rhagoletis pomonella* (Roitberg and Prokopy (1983)). These flies mark fruit with a pheromone after an oviposition. Roitberg and Prokopy (1983) found that there was an increased proclivity to oviposit in marked fruit after modest periods of host deprivation. This kind of behavior can be understood within the framework of dynamic state variable models: host deprivation leads to a reduction in total time available for searching for oviposition sites. Since it is always better to lay an egg than to still have it when $t = T$, fruit which would not be acceptable when there is considerable time available for foraging becomes more acceptable when time is short.

Comparison with other work

The theory closest to the one presented in this paper is the work by Iwasa et al. (1984). They also approach the problem using a dynamic programming formulation but work only in “physiological time”. (Of course, dynamic programming itself is really just a book-keeping technique, so one is almost forced to use it.)

Thus, their methodology could not be used to study host deprivation experiments (although it could obviously be adapted, as in this paper). They provide an easily computed iterative solution of the DPE. The simplification of working in physiological times does not, however, allow one to obtain an explicit analytical solution. On occasion, such analytical solutions can be found; especially if one is willing to resort to approximate methods – see Mangel (1986). The points stressed by Iwasa et al. are (1) effects of forager mortality and (2) effects of limited numbers of eggs on the oviposition decision making. The models developed in this paper treat not only those issues, but also the connection between a physiological state, a reproductive state, and behavior. Although not explicitly stated, the variability of clutch size observed by Charnov and Skinner (1984) or Weis et al. (1983) is also implicit in the theory of Iwasa et al.

Papers by Parker and Courtney (1984), Waage and Godfray (1985), and Weis et al. (1983) are similar to this one in that all three predict fewer eggs per host than the SHM for that host and a relationship between the number of eggs laid on a host and inter-host survival. This papers differs in that the inter-host survival is explicitly tied to demographics and life history effects. Many of the predictions developed by Parker and Courtney (1984) using completely different models (e.g. species with shorter development times should lay bigger clutches, disparity in clutch sizes increases as risk increases, or predictions about the occurrence of super-parasitism) can be obtained using the models developed in this paper. The work of Parker and Courtney is based on four different models, whereas the models developed in this paper are more unified. Finally, there are some predictions that differ. For example, Parker and Courtney (1984, p. 36) predict that clutch size should decrease throughout adult life and refer to certain measurements on butterflies. In contrast, the models developed in this paper show that clutch size need not necessarily decrease with age, but is instead a complicated function of time horizon, previous ovipositional experience, and distribution of hosts.

The papers by Weis et al. (1983) and Waage and Godfray (1985) stress the dependence of clutch size on survival probability from one host to the next. Their theories, however, do not specify how survival probability is related to behavioral decisions or how physiological or reproductive state is tied to behavior decisions.

The theory developed by Charnov and Skinner (1984), (1985) and Skinner (1985) is based on a marginal value type argument. As soon as one introduces handling times for laying eggs in hosts, it is clear that laying clutches that are smaller than the SHM clutch may become optimal. A marginal value rule, however, cannot predict the wide variability of clutch sizes, nor can it be used easily to discuss problems of host deprivation, since there is no allotment for the state of the insect or the total time available for foraging in a theory that is based solely on rates of fitness increase.

Finally, consider the results reported by Godfray (1986) that the most frequently observed clutch for the leaf miner was also the SHM clutch. The explanation provided here is based on an elaboration of Godfray's ideas (Godfray, personal communication). Let $p(c)$ denote the probability that any individual from a clutch of size c , on a host of a certain type survives. Then the expected number of offspring from a clutch of size c is $cp(c)$. For the observations reported by Charnov and Skinner (1984), (1985), $p(c)$ is a decreasing function of c .

A simple model would be $p(c) = 1 - ac$ where a is a constant. The expected number of offspring on a single host would then be $cp(c) = c(1 - ac)$. The individual survivorship is maximized at $c_1^* = 1$, but the expected number of offspring is maximized at $c^* = 1/2a$. For the observations reported by Godfray, on the other hand, $p(c)$ itself has an internal maximum. A simple model would be $p(c) = c(1 - bc)$, with a maximum at $c_1^* = 1/2b$. The expected number of offspring is the $cp(c) = c^2(1 - bc)$ and this has a maximum at $2/3b$. For all intents and purposes the difference between $1/2b$ and $2/3b$ is essentially zero (that is, it will be swamped by other kinds of experimental variation). For the data of Charnov and Skinner, then, there is a “conflict” between individual survivorship and expected number of offspring whereas for the data of Godfray there is no such conflict. This kind of reasoning can be extended to a more general model for $p(c)$ with an internal maximum c_1^* ; the SHM clutch size — that is the value of c that maximizes $cp(c)$ — can then be related to the clutch that maximizes individual survivorship. One can also begin to speculate about when $p(c)$ will have an internal maximum. One speculation (Godfray, personal communication) is that for parasitic insects $p(c)$ will have a maximum at 1 while for herbivorous insects $p(c)$ will have an internal maximum.

In summary, although there is overlap between this paper and previous theoretical work, the application of dynamic state variable models leads to a unifying methodology for dealing with host selection and clutch size problems faced by parasitic insects.

Conclusions and discussions

The use of dynamic state variable modelling allows one to view host site selection and clutch size problems in a way that unifies the physiological state of the organism, the state of the environment and the behavior of the organism. All of the parameters that enter into the state variable models can be directly measured.

Current work involves the simultaneous development of experiment and theory on the relationship between clutch size, host volume and the effect of host deprivation in medfly and on the response of the rose hips fly *Rhagoletis basiola* to marked fruit and the changes in survival of the rose hips fly as a result of behavioral decisions.

Another kind of application of the state variable models developed in this paper involves the evolutionary ecology of tephritid fruit flies. These flies have considerable variation in behavior. For example, the medfly has many generations per year, attacks many kinds of hosts, and lays many eggs per oviposition. The apple maggot has one generation per year, attacks a small number of hosts, and lays one egg per oviposition. The evolutionary ecology of such widely disparate behavioral mechanisms is an interesting problem from both a purely scientific standpoint and also from the perspective of pest management.

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Appendix A: Life history theory and state variable models

In this appendix, life history theory is approached from the viewpoint of dynamic state variable modelling. There is a considerable literature concerned with what can be called “optimal life history theory” — that is, how do organisms make trade-offs in various life history parameters (Boyce (1977), Caswell (1980), Ebert (1985), Goodman (1982), Etges (1982), Lenski and Service (1982), Rago and Dorazio (1984), Schaffer (1974), (1983), Stearns (1976), (1980) and Taylor et al. (1974)). Perusal of this literature shows that without considering a state variable approach, it is extremely difficult to understand what is being traded for what in life history theory. The point of this appendix is to show the natural connection between the ideas of classical demography, life history theory, and dynamic state variable modelling.

To begin, let

$$V(a) = \text{value of future reproduction, starting at age } a. \quad (\text{A1})$$

According to standard demographic theory, one writes

$$V(a) = e^{ra} \sum_{t=a}^w (l_t m_t / l_a) e^{-rt} \quad (\text{A2})$$

where

w = age at the last reproduction

l_t = probability of surviving to age t

m_t = reproduction at age t

r = growth rate of the population.

(For simplicity in what follows, it will be assumed that the population is at a steady state, so that $r = 0$. One of the most difficult questions associated with life history theory, however, is to develop reasonable models from which the value of r can in fact be computed.)

Separating $t = a$ from the rest of the sum and manipulating it gives

$$\begin{aligned} V(a) &= m_a + \left\{ \sum_{t=a+1}^w (l_t m_t / l_a) \right\} (l_{a+1} / l_{a+1}) \\ &= m_a + (l_{a+1} / l_a) V(a+1). \end{aligned} \quad (\text{A3})$$

Equation (A3) is a backwards recursion relationship with the end condition that $V(w) = 0$.

The recursion relationship (A3) can be converted to a DPE by letting m_a and l_a depend upon a strategy set S . Then $V(a)$ is interpreted as the maximum expected reproduction, with the maximum taken over the strategy set. Instead of (A3), one can write

$$V(a) = \max_{s \in S} [m_a(s) + p(a+1, s) V(a+1)] \quad (\text{A4})$$

where

$$p(a+1, s) = \text{Prob}\{\text{living to period } a+1 \mid \text{alive at period } a \text{ and strategy } s \text{ is chosen}\}. \quad (\text{A5})$$

Schaffer (1983) derived an equation analogous to (A4).

If one now introduces a state variable $X(a)$, it is much easier to interpret trade-offs associated with the strategy set. Thus, let m_a and p depend upon a state variable $X(a)$ with dynamics given by

$$X(a+1) = X(a) + f(X(a), s, a) \quad (\text{A6})$$

when strategy s is chosen. Then $V(a)$ is replaced by

$$V(a, x) = \text{maximum reproduction from age } a, \text{ starting with state variable } X(a) = x, \quad (\text{A7})$$

where once again the maximum is taken over the strategy set S . One thus obtains

$$V(a, x) = \max_{s \in S} [m_a(s, x) + p(a+1, s, x) V(a+1, x + f(x, s, a))]. \quad (\text{A8})$$

Equation (A8) is a deterministic dynamic programming equation completely analogous to the stochastic dynamic programming equations discussed in the text.

Appendix B: The completely deterministic situation

The purpose of this appendix is to show that even in a completely deterministic situation it may be optimal to choose clutches smaller than the SHM clutch. That is, that the time and state variable constraints operating on an insect may lead to clutches smaller than the SHM. The thrust of this appendix is to get at the interplay between time horizon and lifetime fitness by eliminating the uncertainties associated with finding hosts and surviving. The idea for this appendix arose in conversations with Colin Clark, and then again with Hugh Dingle. I thank them very much.

Imagine this variant of model 1: The insect starts with a complement of R mature eggs, so that $X(0) = R$, lives with probability 1 for exactly T periods, and in each period encounters with probability 1 exactly the same type of host. Suppose that it lays a clutch of size c in each period. If t is the number of periods in which it oviposits, the lifetime fitness is $tW(c)$, where $W(c)$ is the fitness increment from laying clutch of size c in the host. Clearly one must have that $t \leq T$ and that $tc \leq R$. Other than that, t and c can be viewed as control variables, chosen to maximize lifetime fitness. The following constrained optimization problem arises:

$$\begin{aligned} & \max_{t,c} tW(c) \\ & \text{such that } T - t \geq 0, R - tc \geq 0. \end{aligned} \quad (\text{B1})$$

This problem is easily solved by Lagrange multiplier methods (Wismer and Chattergy 1978). The Lagrangian is

$$L = tW(c) + \lambda(T - t) + \mu(R - tc) \quad (\text{B2})$$

where λ and μ are the Lagrange multipliers associated with the two constraints. The optimality conditions are

$$\begin{aligned} W(c) - \lambda - \mu c &= 0, \\ tW'(c) - \mu t &= 0, \\ \lambda(T - t) = \mu(R - tc) &= 0. \end{aligned} \quad (\text{B3})$$

From these conditions, one immediately sees that if $\mu \neq 0$, then when $t = T$ the optimal clutch size is

$$c^* = R/T \quad (\text{B4})$$

and this becomes smaller as T increases. A complete discussion of the solution will not be given here, but the reader is encouraged to work out the remaining details.

It is instructive to consider some numerical results pertaining to the problem posed in Eq. (B1), since the numerical results shed light on the optimality conditions. Consider fitness functions

$$W(c) = \begin{cases} c(1 - c/K) & \text{logistic} \\ c \exp(-Bc) & \text{Ricker} \end{cases} \quad (\text{B5})$$

where K and B are parameters. The SHM clutches are $c^* = K/2$ for the logistic case and $c^* = 1/B$ for the Ricker case. If a clutch of size c is laid in each period, the total number of clutches laid is the minimum of T and the integer part of R/c . The total fitness is then determined as follows. Let $t^* = \min[T, \text{Int}(R/c)]$ where $\text{Int}(z)$ is the integer part of z . Then the lifetime fitness $F^*(c)$ of a clutch c is

$$F^*(c) = t^*W(c) + W(R - t^*c)H(t^*, T) \quad (\text{B6})$$

where $H(t^*, T) = 1$ if $T > t^*$ and 0 otherwise. Results of computations using Eqs. (B5, 6) are shown in Tables B1 and B2. These results show that even in a completely deterministic setting the state variable constraints may cause clutches smaller than the SHM clutch.

Table B1. Fitness in the completely deterministic setting

c	$X_0 = 150 \quad c^* = 10$ $F^*(c)$ for					
	$T = 10$		$T = 50$		$T = 250$	
	Logistic	Ricker	Logistic	Ricker	Logistic	Ricker
1	9.5	9.0	47.5	45.2	142.5	135.7
2	18	16.4	90	81.9	135	122.8
3	25.5	22.2	127.5	111.1	127.5	111.1
4	32	26.8	120.5	100.8	120.2	100.8
5	37.5	30.3	112.5	90.9	112.5	90.9
6	42	32.9	105	82.3	105.0	82.3
7	45.5	34.7	98.1	75.2	98.1	75.2
8	48	35.9	90.6	68.0	90.6	68.0
9	49.5	36.6	83.4	61.8	83.4	61.8
10	50	36.8	75	55.2	75	55.2

Table B2. Fitness in the completely deterministic setting

c	$X_0 = 150 \quad c^* = 20$ $F^*(c)$ for					
	$T = 10$		$T = 50$		$T = 250$	
	Logistic	Ricker	Logistic	Ricker	Logistic	Ricker
1	9.8	9.5	48.8	47.6	146.3	142.7
2	19	18.1	95	90.5	142.5	135.7
3	27.8	25.8	138.8	129.1	138.8	129.1
4	36	32.7	135.1	123	135.1	123
5	43.8	38.9	131.3	116.8	131.3	116.8
6	51	44.4	127.5	111.1	127.5	111.1
7	57.8	49.3	124.1	106.2	124.1	106.2
8	64	53.6	120.3	101	120.3	101
9	69.8	57.4	116.7	96.3	116.7	96.3
10	75	60.7	112.5	91	112.5	91
11	79.8	63.5	109.5	87.4	109.5	87.4
12	84	65.9	105.9	83.5	105.9	83.5
13	87.8	67.9	102.3	79.6	102.3	79.6
14	91	69.5	98.5	75.6	98.5	75.6
15	93.8	70.9	93.8	70.9	93.8	70.9
16	91.5	69.1	91.5	69.1	91.5	69.1
17	87.3	65.1	87.3	65.1	87.3	65.1
18	84.3	63	84.3	63	84.3	63
19	79.6	58.7	79.6	58.7	79.6	58.7
20	77.5	57.6	77.5	57.6	77.5	57.6

References

- Aoki, M.: Optimization of stochastic systems. New York: Academic Press 1967
- Boyce, M. S.: Population growth with stochastic fluctuations in the life table. *Theor. Pop. Biol.* **12**, 366–373 (1977)
- Browne, R. A.: The costs of reproduction in brine shrimp. *Ecology* **63**, 43–47 (1982)

- Carey, J. R.: Demography and population dynamics of the mediterranean fruit fly. *Ecol. Model.* **16**, 125-150 (1982)
- Carey, J. R.: Host demographic studies of the mediterranean fruit fly. *Ecol. Ent.* **9**, 261-270 (1984)
- Carey, J. R.: Interrelations and applications of mathematical demography to selected problems in fruit fly management, pp. 227-262. In: Mangel, M. et al. (eds.) *Pest control: operations and systems analysis in fruit fly management*. New York, Heidelberg, Berlin: Springer 1986
- Carey, J. R., Vargas, R. I.: Demographic analysis of insect mass rearing: a case study of three tephritids. *Econ. Ent.* **78**, 523-527 (1985)
- Carey, J. R., Krainacker, D. A., Vargas, R.: Life history response of female mediterranean fruit flies, *Ceratitis capitata*, to periods of host deprivation. *Oecologia* (1986)
- Caswell, H.: On the equivalence of maximizing reproductive value and maximizing fitness. *Ecology* **61**, 19-24 (1980)
- Charnov, E. L.: Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**, 129-136 (1976)
- Charnov, E. L., Skinner, S. W.: Evolution of host selection and clutch size in parasitoid wasps. *Florida Entomologist* **67**, 5-21 (1984)
- Charnov, E. L., Skinner, S. W.: Complementary approaches to understanding parasitoid oviposition decisions. *Environ. Ent.* **14**, 383-391 (1985)
- Dunlap-Pianka, H., Boggs, C. L., Gilbert, L. E.: Ovarian dynamics in Heliconiine butterflies: programmed senescence versus eternal youth. *Science* **197**, 487-490 (1977)
- Ebert, T. A.: Sensitivity of fitness to macroparameter changes: an analysis of survivorship and individual growth in sea urchin life histories. *Oecologia* **65**, 461-467 (1985)
- Etges, W. J.: A new review of life history evolution — A response. *Oikos* **38**, 118-124 (1982)
- Fletcher, B. S., Comins, H.: The development and use of a computer simulation model to study the population dynamics of *Dacus oleae* and other fruit flies. *Atti XIV Congr. nat. ital. Ent.*, Palermo, Erice, Bagheria, pp. 561-575 (1985)
- Fritz, R. S., Morse, D. H.: Reproductive success and foraging of the crab spider *Misumena vatia*. *Oecologia* **65**, 194-200 (1985)
- Godfray, H. C. J.: Clutch size in a leaf-mining fly (*Pegomya nigritarsis*: *Anthomyiidae*). *Ecological Entomology* **11**, 75-81 (1986)
- Goodman, D.: Optimal life histories, optimal notation, and the value of reproductive value. *Am. Natur.* **119**, 803-823 (1982)
- Gossard, T. W., Jones, R. E.: The effects of age and weather on egg laying in *Pieris rapae* L. *J. Appl. Ecol.* **14**, 65-71 (1977)
- Heyman, D. P., Sobel, M. J.: *Stochastic models in operations research*, vol. II. New York: McGraw-Hill 1984
- Houston, A. I., McNamara, J. M.: The variability of behavior and constrained optimization. *J. Theor. Biol.* **112**, 265-273 (1985)
- Houston, A. I., McNamara, J. M.: The influence of mortality on the behavior that maximizes fitness in a patchy environment. *Oikos* **47**, 267-274 (1986)
- Iwasa, Y., Suzuki, Y., Matsuda, H.: The theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. *Theor. Pop. Biol.* **25**, 205-227 (1984)
- Jaenike, J.: On optimal oviposition behavior in phytophagous insects. *Theor. Popul. Biol.* **14**, 350-356 (1978)
- Klomp, H., Teerink, B. J.: The significance of oviposition rates in the egg parasite *Trichogramma embryophagum*. *Arch. Neerl. Zool.* **17**, 350-375 (1967)
- Lack, D.: *The natural regulation of animal numbers*. Oxford: Oxford University Press 1954
- Lamberson, R.: Natural selection of life history strategies. *Proc. Third Humboldt Conference on Environmental Systems and Natural Resources*. Humboldt State University, Arcata, Ca. (1986)
- Lenski, R. E., Service, P. M.: The statistical analysis of population growth rates calculated from schedules of survivorship and fecundity. *Ecology* **63**, 665-662 (1982)
- Loschiavo, S. R.: Effect of oviposition sites on egg production and longevity of *Trogoderma parabile* (Coleoptera: dermestidae). *Can. Ent.* **100**, 86-89 (1964)
- Mangel, M.: *Decision and control in uncertain resource systems*. New York: Academic Press 1985
- Mangel, M.: Solution of functional difference equations from behavioral theory. *J. Math. Biol.* **24**, 557-567 (1986b)
- Mangel, M.: Modelling behavioral decisions of insects. To appear in: Cohen, Y. (ed.) *Application of control theory in ecology*. *Proceedings 1986 (Lect. Notes Biomath. 1987)*

- Mangel, M., Clark, C. W.: Towards a unified foraging theory. *Ecology* **67**, 1127–1138 (1986)
- Mitchell, R.: The evolution of oviposition tactics in the bean weevil, *Callosbrochus maculatus*. *Ecology* **56**, 696–702 (1975)
- Parker, G. A., Courtney, S. P.: Models of clutch size in insect oviposition. *Theor. Pop. Biol.* **26**, 27–48 (1984)
- Pianka, E. R.: Natural selection and optimal reproductive tactics. *Am. Nat.* **609**, 453–464 (1976)
- Price, P. W.: General concepts on the evolutionary biology of parasites. *Evolution* **31**, 405–420 (1977)
- Rago, P. J., Dorazio, R. M.: Statistical inference in life-table experiments: the finite rate of increase. *Can. J. Fish. Aqu. Sci.* **41**, 1361–1374 (1984)
- Roitberg, B. D., Prokopy, R. J.: Influences of intertree distance on foraging behavior of *Rhagoletis pomonella* in the field. *Ecol. Ent.* **7**, 437–442 (1982)
- Roitberg, B. D., van Lenteren, J. C., van Alphen, J. J. M., Galis, F., Prokopy, R. J.: Foraging behavior of *Rhagoletis pomonella*, a parasite of hawthorn (*Crateagus viridis*), in nature. *J. Anim. Ecol.* **51**, 307–325 (1982)
- Roitberg, B. D., Prokopy, R. J.: Host deprivation influence on response of *Rhagoletis pomonella* to its oviposition deterring pheromone. *Physiol. Ent.* **8**, 69–72 (1983)
- Roitberg, B. D., Prokopy, R. J.: Host visitation sequence as a determinant of search persistence in fruit parasitic tephritid flies. *Oecologia* **62**, 7–12 (1984)
- Roitberg, B. D., Cairl, R. S., Prokopy, R. J.: Oviposition deterring pheromone influences dispersal distance in tephritid fruit flies. *Ent. Exp. Appl.* **35**, 217–220 (1984)
- Schaffer, W. M.: Optimal reproductive effort in fluctuating environments. *Am. Natur.* **108**, 783–790 (1974a)
- Schaffer, W. M.: Selection for optimal life histories: the effects of age structure. *Ecology* **55**, 291–303 (1974b)
- Schaffer, W. M.: The application of optimal control theory to the general life history problem. *Am. Natur.* **121**, 418–431 (1983)
- Skinner, S. W.: Clutch size as an optimal foraging problem for insects. *Behav. Ecol. Sociobiol.* **17**, 231–238 (1985)
- Snell, T. W., King, C. E.: Lifespan and fecundity patterns in rotifers. *Evolution* **31**, 882–890 (1977)
- Stearns, S. C.: Life-history tactics: a review of the ideas. *Quart. Rev. Biol.* **51**, 3–47 (1976)
- Stearns, S. C.: A new view of life-history evolution. *Oikos* **35**, 266–281 (1980)
- Taylor, H. M., Gourley, R. S., Lawrence, C. E., Kaplan, R. S.: Natural selection of life history attributes: an analytical approach. *Theor. Pop. Biol.* **5**, 104–122 (1974)
- van Alphen, J. J. M.: Aspects of the foraging behavior of *Tetrastichus asparagi* Crawford and *Tetrastichus spec. (Eulophidae)*, gregarious egg parasitoids of the asparagus beetles *Crioceris asparagi* L. and *C. Duodecimpunctata* L. (*Chrysomelidae*). I. Host-species selection, host stage selection, and host discrimination. *Nether. J. Zool.* **30**, 307–325 (1980)
- van Alphen, J. J. M., Nell, H. W.: Superparasitism and host discrimination by *Asobara tabida nees (Braconidae: alysiinae)*, a larval parasitoid of drosophilidae. *Nether. J. Zool.* **32**, 232–260 (1982)
- Waage, J. K., Godfray, H. C. J.: Reproductive strategies and population ecology of insect parasitoids, pp. 449–470. In: Sibly, R. M., Smith, R. H. (eds.) *Behavioural ecology*. Oxford: Blackwell Scientific Publications 1985
- Waage, J. K., Ming, N. S.: The reproductive strategy of a parasitic wasp. *J. Anim. Ecol.* **53**, 401–415 (1984)
- Weis, A. E., Price, P. W., Lynch, M.: Selective pressures on clutch size in the gall maker *Asteromyia Carbonifera*. *Ecology* **64**, 688–695 (1983)
- Wiklund, C.: Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* (Lepidoptera). *Oikos* **28**, 56–68 (1977)
- Williams, G. C.: Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**, 398–411 (1957)
- Wismer, D. A., Chattergy, R.: Introduction to nonlinear optimization. New York: North Holland 1978

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