State dependent problems for parasitoids: case studies and solutions

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Abstract

Many problems that parasitoids face in nature are state-dependent. For example, the optimal decision regarding encounters with already-parasitized hosts often depends upon the egg load (egg state) of the focal organism. Furthermore, many biologically relevant events (e.g., host encounters) occur with some probability. Thus, an appropriate model for analyzing such problems is a stochastic state variable model, with Dynamic Programming (DP) as the appropriate tool to derive an optimal policy (Together known as SDP). In this paper, we consider two case studies where SDP models provide solutions to parasitoid foraging problems. These include, optimal attacks on target and non-target hosts in the context of biological control as well as optimal attacks on hosts of known size but unknown instar. Using these case studies, we show a rather general form of DP, and its infinite horizon form for which we discuss algorithmic solution methods, as the DP equation is not constructive in that case. The application to life time processes induces a slight generalization of classical infinite horizon DP. We also stress that, using Kolmogorov's equation, essentially the same computer code that lets one compute an optimal policy can be used to compare its efficiency against that of other policies, avoiding lengthy simulations.

1 Introduction

It is becoming increasingly clear that many parasitoid behaviors are state dependent. As just a sample of many such relationships, Ueno (1999) and Sirot et al. (1997) showed that oviposition decisions (superparasitism) depend upon eggload

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(egg state), Desouhant et al. (2005) showed that feeding decisions depend on nutrition state, Roitberg et al. (1993) demonstrated that host discrimination can be a function of information state, while Wajnberg et al. (2006) showed that patch leaving decisions are a function of age.

Of course, one could go on citing many other examples, but the important question that emerges is: how does one incorporate such states into predictions of parasitoid behaviour? The answer can be found in the form of Stochastic Dynamic Programming models (Bellman 1957). Though these models were first developed to solve problems in human economics, they have now been adapted to address issues in natural non-human systems, including parasitoids, thanks to the efforts of Clark & Mangel (2000), Houston & MacNamara (1999) and others. The models take many forms but in general, optimal decisions are calculated based upon maximizing expected lifetime reproductive success (the most common fitness proxy see Roitberg et al. 2001) as a function of current state(s). As noted above, this state dependant theory has shown great utility for predicting a variety of parasitoid behaviours. In particular, of late dynamic programming models have been employed to solve a number of parasitoid problems, including: (1) patch time allocation (see review by Wajnberg 2006), (2) egg versus time limitation (Rosenheim 1999, Ellers et al. 2000), (3) oviposition decisions (Mangel 1989) and (4) host feeding (Collier 1995).

Dynamic programming models have been reviewed elsewhere and, as such, we refer readers to Houston et al. (1988) for background reading. Here we will use this opportunity to show readers in detail how to formulate and analyze dynamic programming models. To do so, we have chosen two classic problems in parasitoid behavioral ecology, optimal fidelity and optimal instar discrimination. These problems provide a kind of window into state variable challenges that parasitoids typically face. We shall also show how the same formulation, in terms of dynamic state models, lets one replace Monte-Carlo simulations by a faster and more precise approach, namely Kolomogorov's equation, which turns out to have a close kinship with Bellman's equation.

Fidelity

In biological control, one of the big questions that researchers face is the possibility of attacks on non-target hosts (Bigler et al. 2006). Thus, the key issue here is fidelity *i.e.*, will the agent restrict its attacks to targets (as chosen by the biocontrol practitioner)? As noted above, there already exists considerable theory on optimal host selection and this question neatly falls into that category *i.e.*, are there conditions where the parasitoid will attack (presumably) the lower quality, non-target host? It is difficult to provide a general answer for biological control practitioners because this answer is likely to be context-dependent with the context here being life history. However, as a simple starting point and drawing from Roitberg (2000) we will consider two major categories of parasitoids, those that are proovigenic versus those that are synovigenic. The former types are comprised of individuals who begin adult life with a full complement of eggs and then deplete those eggs over time through parasitizing hosts. The latter individuals continually mature new eggs following eclosion. In the former case, each time an egg is laid, the parasitoid will move into the future with one less egg available than before oviposition compared to the latter whereupon future egg availability will depend upon egg maturation rates and ovarioles. Further, we must consider gregarious parasitoids *i.e.*, individuals not only have to "decide" whether to accept or reject hosts but also with acceptance they must decide how many eggs to lay in a given host (*e.g.*, Hoffmeister et al. 2005). Here is the scenario that we consider: An individual forages within a large non-depleting universe of hosts. When hosts are encountered, target hosts are accepted with requisite clutch size decision but when non-target hosts are encountered, acceptance/rejection decisions are required. Below, we develop a theory for non-target host acceptance decisions.

Size discrimination

Many parasitoids choose hosts on the basis of size (*e.g.*, Wang & Messing 2004). Size is a useful criterion because it often correlates well with nutrient content (Vinson & Iwantsch 1980) and host defensive ability (Gerling et al. 1990). However, when parasitoids are koinobionts wherein their larvae exploit developing hosts, then host instar is also extremely important due to differences in growth rates and time limitations. This should not pose a problem for parasitoids that are host specialists because size and instar are highly correlated. However, when parasitoids are generalists, they may encounter a vast range of different sized individuals within the same instar. So, how should koinobiont parasitoids choose hosts?

This question arises from work being conducted by Henry et al. (2005, 2006). Henry works with the parasitoid *Aphidius ervi*, a generalist wasp that attacks a variety of aphids. It turns out that, regardless of host species, instars 2 and 3 are the best hosts and 1 and 4 are often unsuitable. In addition, independent of host species, the larger the aphid, the more dangerous that aphid is to *A. ervi* via his defensive maneuvers, *e.g.* kicking. These two factors are interesting in of themselves but they become complicated in that there is no obvious manner by which the parasitoid can determine instar across host species, especially if size is the criterion employed. For example, for the pea aphid *Acyrthosiphon pisum*, the high quality second instar is approximately the same size as the low quality fourth instar of the foxglove aphid *Aulacorthum solani* and as noted above, Henry et al. 2005 suggests that *A. ervi* cannot identify instar directly and probably uses sized-based cues. As such, there are six distinct size classes when one combines foxglove and pea aphids of different instars. Let af(i) and ap(j) denote the i-th instar and the j-th instar of foxglove and pea aphids respectively, the six classes are [af(1)]; [af(2)]; [*af(3), ap(1)*]; [*af(4), ap(2)*]; [ap(3)]; [ap(4)]. The italicized classes above indicate possible misidentification of species, and could thus be problematic. So, what should the parasitoid do? Of course, the problem is complicated by parasitoid state in that identification errors are more costly when eggload is low than when it is high. We develop a model that specifically incorporates possible misidentification into host acceptance policy.

2 Egg laying decision problems

2.1 Fidelity: proovogenic gregarious parasitoids

Designing a (discrete-time) state variable model

Identify

1. the *stages* of the process,
2. the *control variables*, those that have to be “chosen” at each stage
3. the *disturbances* and the probability laws governing them,
4. the *state variables*, i.e. the necessary information at any given stage to let one compute the future evolution of the system if the future control and disturbance variables are known,
5. the *dynamical equation* giving the state at stage $k+1$ as a function of state, control and disturbances at stage k.

Designing an dynamical optimization problem

With the state variable model, write the benefit accrued (or cost incurred) at each stage as a function of that stage’s variables and, if any, the terminal benefit (or cost) as a function of terminal state. The criterion to be maximized (or minimized) should be the sum of all of these.

2.1.1 The model

We now describe the fidelity problem in the formalism of a state variable dynamic system and a criterion to be maximized. Classically, the decisision variables themselves may depend on some current information. Here, the available information at any stage will be the current state, a considerable simplification of the theory.

Dynamics Let

- $t \in [0, \infty) \subset \mathbb{R}_+$ the current time, a state variable here,
- $x \in \{0, 1, \dots, X\} \subset \mathbb{N}$ the number of eggs available, a state variable,
- $c \in \{0, 1, \dots, x\}$ the clutch size in a given host, the decision variable,
- $h(c)$ the "handling time" it takes to lay a clutch of size c (with $h(0) = 0$),
- T, a random variable, the travel time to the next host encounter.

The variables t, x, c, and T take on new values for each of the encounters of the parasitoid with a host. Let t_k, x_k, c_k, and T_k be the value they have at the encounter number k, $k \in \mathbb{N}$. The whole sequence of the c_k's will be written as $\{c_k\}$ and likewise for other variables.

Trivially, these variables obey the following dynamical equations:

$$\begin{aligned} t_{k+1} &= t_k + h(c_k) + T_k \,, \\ x_{k+1} &= x_k - c_k \,. \end{aligned}$$

Criterion Let

- $\omega \in \{\mathcal{T}, \mathcal{N}\mathcal{T}\}$ the nature of the host encountered, $\mathcal{T}$arget or $\mathcal{N}$on $\mathcal{T}$arget, a random variable (there could be an arbitrary number of host types in this model),
- $\lambda_{\mathcal{T}}$ and $\lambda_{\mathcal{N}\mathcal{T}}$ the probabilities that $\omega = \mathcal{T}$ or $\omega = \mathcal{N}\mathcal{T}$ respectively,
- $\xi(t) \in \{0, 1\}$ the life status indicator, equal to 1 if the parasitoid is alive at time t, 0 if it is dead, a random variable,
- $P(t)$ the probability that $\xi(t) = 1$, or the expectation of ξ,
- $f(\omega, c)$ the fitness gained, say the expected number of offspring, as a function of the nature of the host and the clutch size. It is assumed to be increasing and concave, with $f(\omega, 0) = 0$, and bounded by some positive $f_{\max}(\omega)$.

Again, we shall consider sequences of values of the variables $\{\omega_k\}$.

The "decision" to lay c eggs at a given stage may bring less fitness than $f(\omega, c)$, because the parasitoid may die before it has laid its c eggs. We therefore consider the conditional expected utility of that decision given that it is alive at time t. To do so, introduce the ratio ρ defined as:

$$\rho(t, \tau) = \frac{P(t+\tau)}{P(t)}$$

which is the probability of the parasitoid surviving until the time $t+\tau$ conditioned on its being alive at time t. The conditional expected utility sought is then:

$$g(\omega, t, c) = \sum_{\ell=1}^{c} [f(\omega, \ell) - f(\omega, \ell - 1)]\rho(t, h(\ell))\,.$$

Obviously, one has:

$$\forall \omega, t, c, \quad 0 \le g(\omega, t, c) \le f(\omega, c)\,,$$

and therefore also:

$$\forall \omega, t, \quad g(\omega, t, 0) = 0\,.$$

The foraging activity ends when the parasitoid dies, a random variable, so that we do not know *a priori* the number of encounters to be considered, nor even a bound on that number (although for a realistic set of data, a bound could be found for any practical purpose). We therefore take the criterion to be maximized as

$$J(t_0, x_0; \{c_k\}) = \mathbb{E} \sum_{k=0}^{\infty} \xi(t_k) g(\omega_k, t_k, c_k)\,.$$

Parallel with Charnov's patch leaving problem

The problem considered here is completely equivalent to Charnov's classical patch leaving problem (Charnov, 1976) for a solitary parasitoid, up to the exact shape of the fitness function which may differ. As a matter of fact, we have the correspondence shown in Table 1 (the function $\tilde{f}$ is defined hereafter):

Fidelity	Patch leaving
Host	Patch
Time $h(c)$ to lay c eggs	Time t spent on the patch
Type of host ω	Quality of the patch
Fitness gain $f(\omega, c)$	Cumulative umber of eggs laid $\tilde{f}(\omega, t)$
Travel time	Travel time

Table 1: Parallel between the fidelity and patch leaving problems.

The number of eggs laid in Charnov's problem is classically given as a function, here $\tilde{f}$, of the time t spent on the patch. To relate it to the clutch size c, we notice that $h(c)$ being strictly increasing, to any given time t corresponds formally a clutch size $c = h^{-1}(t)$ (the largest clutch size c such that $h(c) \leq t$). Thus we let $\tilde{f}(\omega, t) = f(\omega, h^{-1}(t))$. Hence the analytic form commonly used in the patch leaving problem has no reason to hold here, but the only important point in the theory is that this function be concave. This is insured in the patch leaving problem by search efficiency decrease due to patch depletion, and in the fidelity problem by the law of decreasing return of eggs laid.

As a consequence, the work presented here may be viewed in a large extent as an extension of that of Wajnberg et al. (2006) to proovigenic parasitoids, and we treat it in a similar way.

2.1.2 Dynamic programming

From the above description, we can derive Bellman's Dynamic Programming equation. Classically, we let:

$$G(t_0, x_0) = \max_{\{c_k\}} J(t_0, x_0; \{c_k\}) , \tag{1}$$

and notice that the problem is stationary in the sense that G does not depend on the number of the initial stage.

The decision variable c_k may depend on x_k and ω_k, and on $\xi(t_k)$ which is known as a consequence of Descartes' law "cogito, ergo sum", but not on T_k which is not known at time t_k. Hence, we get:

$$G(t, x) = \mathbb{E}_{\omega,\xi} \max_{c \leq x} \mathbb{E}_T [G(t + T + h(c), x - c) + \xi(t) g(\omega, t, c)] .$$

Notice, first,, that there is no loss of performance in requesting that the decision taken is the same whether the parasitoid is dead or alive, since our formulation allows for a decision taken by a dead parasitoid but with no effect on the performance. Hence, we may shift the $\mathbb{E}$xpectation operator in ξ to the right of the max operator and inside the square bracket, resulting in:

$$G(t, x) = \mathbb{E}_{\omega} \max_{c \leq x} [\mathbb{E}_T G(t + T + h(c), x - c) + P(t) g(\omega, t, c)] . \tag{2}$$

In this equation, $G(t, x)$ is the maximal expected fitness gained from time t on, if $x(t) = x$. The equation means that the forager has to balance the benefit expected from laying more eggs, *i.e.*, increasing c and thus $g(\omega, t, c)$, against the loss in future ability to gain fitness, measured through the decrease in the function G due to the decreasing egg load $x - c$ available.

Now, $G(t,x)$ is an *a priori* expectation. If, say, the probability of being alive at time t is very small, then $G(t,x)$ will accordingly be very small. It turns out to be preferable for some purposes to work with the conditional expectation, given that the parasitoid is alive at time t. Let

$$F(t,x) = \frac{1}{P(t)} G(t,x) \tag{3}$$

be that conditional expectation.

Dividing through equation (2) by $P(t)$, we get:

$$F(t,x) = \mathbb{E}_\omega \max_{c \le x} [\mathbb{E}_T \rho(t, T + h(c)) F(t + T + h(c), x - c) + g(\omega, t, c)] \,. \tag{4}$$

Notice that, since ω assumes only two values, the expectation operator in ω can be decomposed as:

$$\begin{aligned} F(t,x) = \lambda_{\mathcal{T}} \max_{c \le x} [\mathbb{E}_T \rho(t, T + h(c)) F(t + T + h(c), x - c) + g(\mathcal{T}, c)] \\ + \lambda_{\mathcal{NT}} \max_{c \le x} [\mathbb{E}_T \rho(t, T + h(c)) F(t + T + h(c), x - c) + g(\mathcal{NT}, c)]. \end{aligned} \tag{5}$$

That forms displays the fact that different decisions may be taken for different host types, since there is a $\max_c$, hence a separate choice of c, for each type.

Now, the test of fidelity is that, $\forall c \in \{1, \ldots, x\}$,

$$\mathbb{E}_T \rho(t, T + h(c)) F(t + T + h(c), x - c) + g(\mathcal{NT}, c) < \mathbb{E}_T \rho(t, T) F(t + T, x) \,, \tag{6}$$

which means that for any non-zero clutch size, the expected fitness gained from laying eggs in a non target host is less than that gained by bypassing this host. However, the measure of the fitness gained is in terms of the function F, solution of Bellman's equation, so that performing this test requires to solve that equation.

2.1.3 Solving Bellman's equation

The process of solving Bellman's equation is usually a numerical one, since there is no reason why there should exist a closed form solution for realistic data. This is a functional equation, therefore not easy to solve. There are classically two algorithms used to solve it, both iterative, called *iteration on the value* —or *Howard's algorithm*—, and *iteration on the policies*. (These are just names.) The second one is known to converge faster, but it is so much more complex to program that we shall stick here with the simpler Howard's algorithm. To a mathematician, this is a simple Picard iteration for the fixed point equation (2) or (4). It can also be understood as the limit of a finite horizon Bellman iteration process as the horizon becomes very large. It looks simpler written for G, but the fact that G may take very small values may make it numerically ill-behaved. If there is a possibility of computing $\rho(t,\tau)$ with reasonable accuracy, even for "large" t, then the following algorithm is better-behaved. We denote F^n, $n = 0, 1, \ldots$ the successive aproximations of F.

$$F^0(t,x) = 0\,,$$
$$F^{n+1}(t,x) = \mathbb{E}_\omega \max_{c\le x}[\mathbb{E}_T \rho(t, T + h(c))F^n(t + T + h(c), x - c) + g(\omega, t, c)]\,. \tag{7}$$

The expectation in ω can be decomposed as in equation (5). Since c ranges over a finite and presumably rather small set, the maximization can be performed by simply computing the bracket for each possible value of c and keeping the best. As for the expectation in T, it is with respect to a scalar variable, so that the most efficient method is to use a simple integration scheme such as the trapezoidal rule.

We notice that this algorithm presents the desirable feature that all approximations F^n satisfy $F^n(t,0) = 0$ for all t. Thus, so does the limit, as it should.

We offer the following theorem, which is a slight extension of a classical result for Bellman's stationary equation:

Theorem 1 *If there exists $r < 1$ such that $\rho(t, t+T)$ is almost surely less or equal to r, then*

1. *equations (2) and (4) have a unique bounded solution G or F, respectively,*
2. *these solutions coincide with the definitions (1) and (3), respectively, and the maximization operator in (2) or, equivalently (4), yields the optimal strategy,*
3. *The sequence F^n converges uniformly to the unique solution of the corresponding Bellman equation and so does the equivalent recursion for G.*

An hypothesis that insures that $\rho(t,T)$ be almost surely bounded is the following:

Hypothesis 1

1. *T is almost surely larger than or equal to some positive T_0,*
2. $P(t + T_0)/P(t) \le r$

The first of the above two properties suffices to insure convergence of Howard's algorithm in another realsitic case:

Theorem 2 *If the lifetime of the parasitoid is almost surely less than a fixed positive number L, and if the first hypothesis above holds, then we have the same conclusions as in theorem 1.*

Numerical experiments

We have conducted a limited set of numerical experiments to validate the methodology, and draw some early biological conclusions.

We have used the following parameters, that are not specific to any particular system but are well within range of many parasitoids species: :

- computational horizon: 36 hours,
- handling time: 1 minute per egg (*i.e.* proportional to c),
- initial eggload ≤ 144,
- fitness law $f(\omega, c) = f_{\max}(\omega)(1 - \exp(-c/\pi))$ with $\pi = 2.5$,
- $c_{\max}$= 10 (level beyond which superparasitism would reduce the fitness gain by threatening the survival of the host, or severely decreasing survivorship of parasitoid larvae via competition),
- relative fitness value of target vs. non target hosts for a clutch of any given size: 5,
- law of travel time: exponential with an expectation of 30 minutes, truncated at $T \geq 1$min,
- survival law: Weibull law with scale parameter: 12 hours, shape parameter: 4,
- frequency of target hosts vs. non targets: 4.

We stopped the algorithm when the precision has reached 0.01. The results are depicted in figures 1 and 2.

There are several aspects in these results that are relevant to biological concerns regarding non-target effects when the target (the pest insect) is common relative to non-targets favour and would be particularly pertinent to situations where non-targets are rare, threatened species (Lynch et al. 2002). First, notice that, as expected, the optimal clutch size varies as a function of age and eggload. By contrast, and similar to that of solitary parasitoids (Roitberg 2000), there are conditions under which the optimal response to non-target hosts will be rejection. These are the conditions that biological control workers should strive to create. Second, the optimal clutch size for attacks on target hosts largely tracks eggload up the maximum, is nearly independent of age for young but not old parasitoids, and almost always exceeds that of optimal clutch size on non-targets, eggload constraints notwithstanding. This is a good thing from a biological control perspective especially if damage to hosts (*i.e.* via mortality or fecundity) is clutch-size dependent. What the figures also tell us is that parasitoid rejection of non-target can be accomplished by releasing specialist biocontrol agents that have relatively low egg loads or are long-lived, relative to egg load (cf. Louda et al. 2003). An important caveat is that once the parasitoid has attacked some hosts the problem becomes both frequency dependent and strongly linked to population dynamics.

2.1.4 The stationary case

We turn now to a simpler situation where we can derive more analytical results from dynamic programming. Assume that,

1. the parasitoids are not egg-limited, having a large enough initial egg load,
2. the survival law is exponential $P(t) = \exp(-\rho t)$, with a fixed intensity ρ,

and, to simplify the calculations, the less critical hypotheses that,

3. the time to lay eggs is proportional to the number of eggs laid, *i.e.* $h(c) = hc$, h a positive constant,
4. the random variable T has a bounded support $[0, T_{\max}]$.

Because of the first hypothesis, the egg state is no longer a factor, and F is not a function of x anymore. Thanks to the second hypothesis, $\rho(t,\tau) = \exp(-\rho\tau)$ with a fixed parameter ρ, thus it is independent from t. It is convenient to introduce the parameter

$$\Theta = \mathbb{E}\mathrm{e}^{-\rho T}\,.$$

Then F will also be constant, satisfying the stationary Bellman equation

$$F = \mathbb{E}_\omega \max_c [\Theta \mathrm{e}^{-\rho h c} F + g(\omega, c)]\,. \tag{8}$$

If we accept the hypothesis of decreasing return of the eggs laid in a single host, the maximum in (8) above is reached at:

$$c^*(\omega) = \min\{c \mid \Theta \mathrm{e}^{-\rho h c} F + g(\omega, c) - \Theta \mathrm{e}^{-\rho h (c+1)} F + g(\omega, c+1) \le 0\}\,.$$

Or, using the definition of g above, and after a simple calculation

$$c^*(\omega) = \min\{c \mid f(\omega, c+1) - f(\omega, c) \le \Theta F(\mathrm{e}^{\rho h} - 1)\}\,.$$

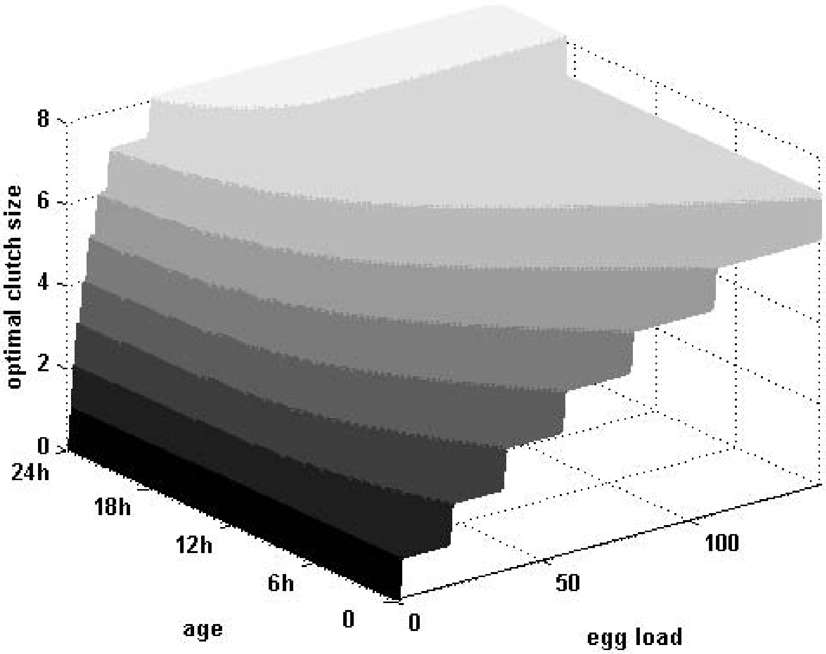

Figure 1: The optimal clutch size from attacks on target hosts by proovigenic parasitoids as a function of egg load and age.

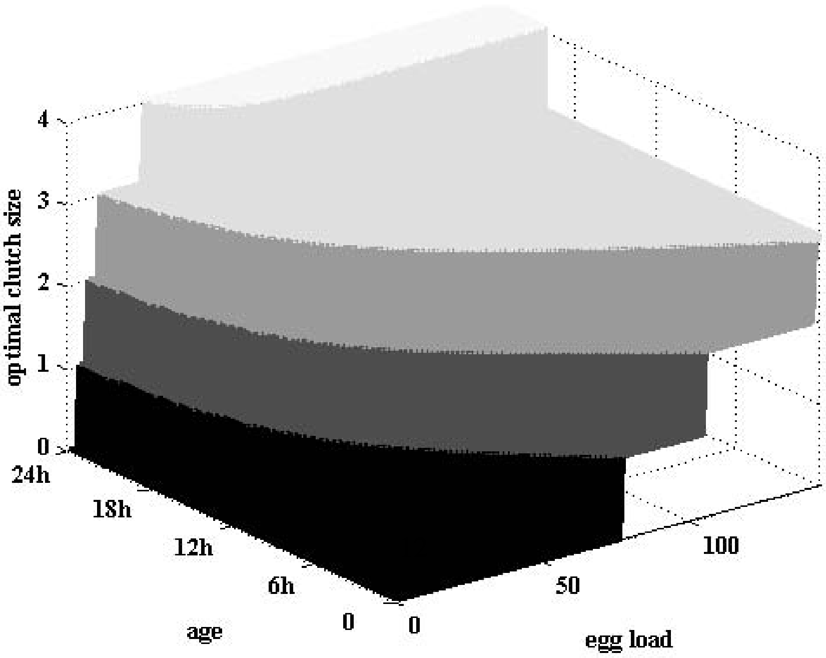

Figure 2: The optimal clutch size from attacks on non-target hosts by proovigenic parasitoids as a function of egg load and age.

In order to investigate the effect of the mortality rate, we expand the above equations in the neighborhood of $\rho = 0$, hence letting $\exp(\rho h) \simeq 1 + \rho h$. The above eqution becomes:

$$c^*(\omega) = \min\{c \mid \frac{f(\omega, c+1) - f(\omega, c)}{h} \leq \Theta\rho F\}\,. \tag{9}$$

Let the optimal c be $c^*(\omega)$, and write $\bar{c}$ for its expectation, and $\bar{g} = \mathbb{E}_\omega g(\omega, c^*(\omega))$ for the expectation of g. It is a simple matter to see that (8) now reads

$$F = F\Theta(1 - \rho h\bar{c}) + \bar{g}\,.$$

Furthermore, the hypothesis that T is bounded by some $T_{\max}$ lets us expand $\Theta \simeq 1 - \rho\bar{T}$ where $\bar{T}$ is the expected value of T. As a result, we get

$$\rho F \simeq \frac{\bar{g}}{\bar{T} + h\bar{c}}\,. \tag{10}$$

This equation has several consequences.

First, notice that, as ρ goes to zero and if we let γ be the limit foraging rate, F converges to $\int_0^\infty \exp(-\rho t)\gamma \mathrm{d}t = \gamma/\rho$, so that ρF converges to γ, while g converges to f, and, of course, Θ converges to 1. Hence, in the limit as $\rho \to 0$, equations (9) and (10) are just just Charnov's Marginal Value Theorem (MVT), stating that the parasitoid should leave the resource it is exploiting when the intake rate is about to drop below the optimal overall mean intake rate in the environment. Thus for very small mortality rate, simple rate maximizing is optimal (Mangel 1989).

Second, it shows that, as ρ varies, ρF can only decrease, since the ratio $\bar{f}/(\bar{T} + h\bar{c})$ is maximal at the MVT solution. Hence, since Θ is also decreasing with ρ, in equation (9), the right hand side (r.h.s.) decreases as ρ is increased from 0 to a positive value. According to the law of diminishing return, this means that $c^*(\omega)$ has to increase for all types of hosts.

2.1.5 Evaluating the selective pressure

The "optimal" behaviour determined by the above theory is more likely to approximate the real behaviour of parasitoids in that it gives likely a larger fitness superiority over simpler behaviours. It is therefore important to be able to evaluate this difference. The Dynamic Programming theory gives us $G(0, x_0)$ which is the expected fitness acquired under the optimal strategy for an initial egg load of x_0. We need now to evaluate the fitness gained using other strategies. (*e.g.*, Roitberg & Mangel 1997)

A classical means of evaluating this is via Monte-Carlo simulation runs with the assumed simpler strategy $c(\omega, t, x)$. We note here that there is a simpler, faster, and more precise way of doing that. According to Kolmogorov's equation, the expected efficiency of a given strategy $c(\omega, t, x)$ is a solution of the same equation (2), without the $\max_c$ operator, when plugging our $c(\omega, t, x)$ in the right hand side instead of the optimal c^*. As a consequence, the corresponding Howard's algorithm converges to the desired fitness expectation. The same computer code can be used, replacing the max operation by the choice of the given decision strategy. It is therefore much faster and more acurate in that role. (With some more work, one may also obtain the variance of the fitness gained by a similar procedure.)

Another valuable check would be to compare the optimal fitness gain with the optimum obtained if the parasitoid does not discriminate $\mathcal{T}$ from $\mathcal{NT}$ hosts. This is obtained by almost the same computation, just interchanging the $\max$ and $\mathbb{E}$ operators in the r.h.s. of Bellman's equation (4). See section 2.3 for more details.

With the parameters chosen in figures 1 and 2, the corresponding optimal clutch size for the "blind" parasitoids is shown in figure 3.

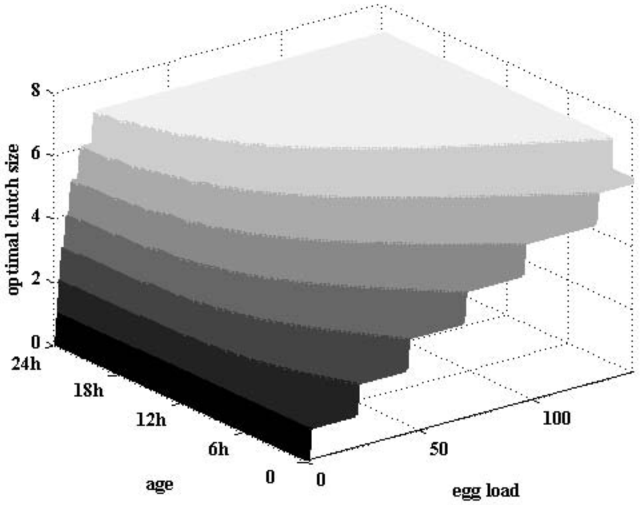

Figure 3: The optimal clutch size from attacks on all hosts by a so-called "blind" proovigenic parasitoid that cannot discriminate target from non-target hosts. The optimal clutch varies as a function of egg load and age.

The ratio of fitness obtained in the blind behaviour to that of the optimal behaviour is above 98%, indicating that the "optimal" behaviour has very little selective benefit. This result, though, is very much dependant on the parameters. Figure

4 gives a plot of this dependance.

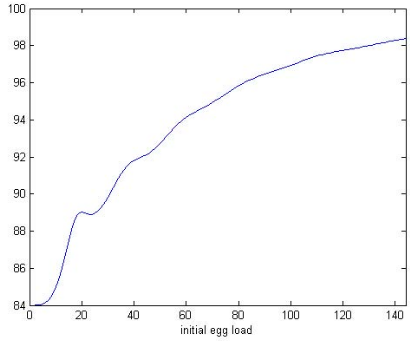

Figure 4: Relative efficiency of a “blind” parasitoid that cannot discriminate target from non-target hosts as a function of initial egg load

We see that, *e.g.*, with a smaller initial eggload of 30, this ratio drops below 90%.

2.2 Fidelity: synovigenic gregarious parasitoids

We turn now to the case of a parasitoid still having a predetermined egg load, but immature. Eggs mature at a fixed rate of m eggs per unit time, and mature eggs are available to be laid. We assume that egg maturation does not impact the mortality rate, but see Roitberg (1989).

2.2.1 Model and dynamic programming

Let $y(t)$ denote the number of immature eggs left at time t, and $y_0 = y(0)$. Since we assume that the egg maturation rate is constant, we have:

$$y(t) = \max\{y_0 - mt, 0\}\,.$$

As a simple function of t, we do not need to make it an extra state variable. We shall write the dynamics in terms of the “state” variables t and x, the control variable c and the random variable T. Let for any τ

$$\delta(t,\tau) = \min\{y(t), m\tau\} = \min\{\max\{y_0 - mt, 0\}, m\tau\}\,.$$

This expression looks awkward, but it can be interpreted as a “saturation” function:

$$\delta(t,\tau) = \left\{\begin{array}{lll} 0 & \text{if} & y_0 - mt \le 0\,, \\ y_0 - mt & \text{if} & 0 \le y_0 - mt \le m\tau\,, \\ m\tau & \text{if} & y_0 - mt \ge m\tau\,. \end{array}\right.$$

The dynamics are now

$$\begin{aligned} t_{k+1} &= t_k + h(c_k) + T_k\,, \\ x_{k+1} &= x_k - c_k + \delta(t_k, h(c_k) + T_k)\,. \end{aligned}$$

And we restrict c_k to be no more than x_k.

Two comments are in order here. On the one hand, x_k is no longer an integer here, since the products mt_k and $m(h(c_k)+T_k)$ are not integers. Yet, the constraint $c_k \le x_k$ is correct, insisting that c_k is an integer. That way, an egg "partially matured" is not counted as available.

On the other hand, there is a slight error here, since we restrict c_k to be no more than the number of available mature eggs, but this holds at the beginning of the oviposition on the current host only. It neglects eggs that might mature during the oviposition. Yet, this should be a very good approximation for most systems (Godfray 1994).

If there is no lower bound on possible values of the random variable T, we cannot give an *a priori* bound on the number of host encounters. So we, again, use infinite-stage dynamic programming. Using the same notations as previously, the dynamic programming equation now reads

$$F(t,x) = \mathbb{E}_\omega \max_{c \le x} \mathbb{E}_T[\rho(t, h(c){+}T)F(t{+}h(c){+}T, x{-}c{+}\delta(t, h(c){+}T)) + g(\omega, t, c)].$$

The numerical procedure and convergence theorems follow as previously, *mutatis mutandis*.

Here again, we have run a few numerical experiments to validate the theory. We have used the same parameters as for the proovigenic case, with furthermore a maturation rate of one egg per 10 minutes. Results are given in figures 5 and 6. What we now see is that,, qualitatively, the clutch size policies for attacks on target and non target hosts is similar but optimal clutch size is almost always lower on non-targets. The contrast in policies for these gregariouis synovigenic vs. proovigenic parasitoids is analagous to the significant differences Roitberg (2000) found for solitary wasps with different reproductive strategies. Once again, we find that there are abrupt changes or step functions in optimal clutch size due to the interaction between egg maturation rates and expectation of life for synovigenic parasitoids compared to the nearly monotonic policies when individuals are proovigenic and, as before, we caution against release of such organisms without very thorough studies of host acceptance policies.

2.3 Size acceptance policy

We now turn to a problem with imperfect information, but easy to handle. In that problem, we deal with a solitary parasitoid, *i.e.*, there is no clutch size decision to

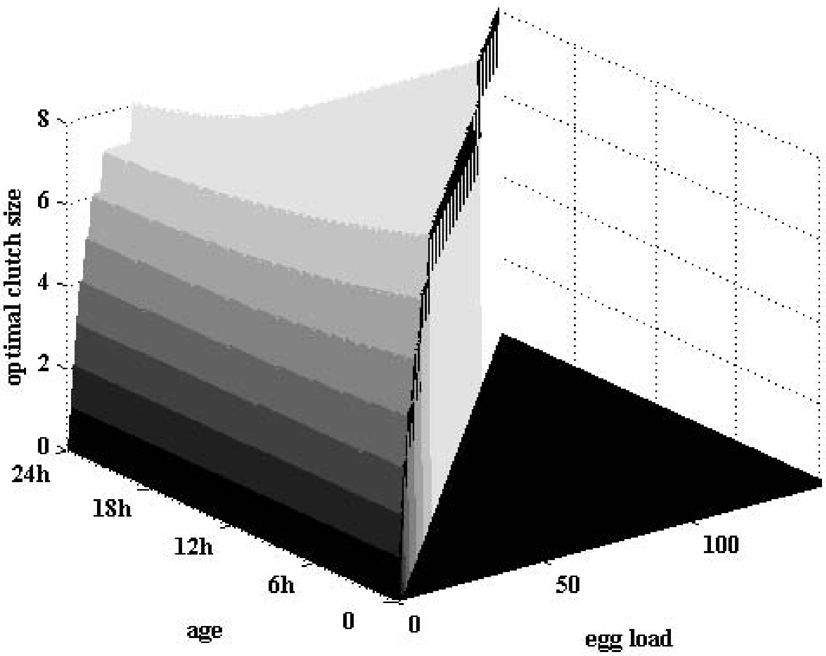

Figure 5: The optimal clutch size from attacks on target hosts by synovigenic parasitoids as a function of egg load and age.

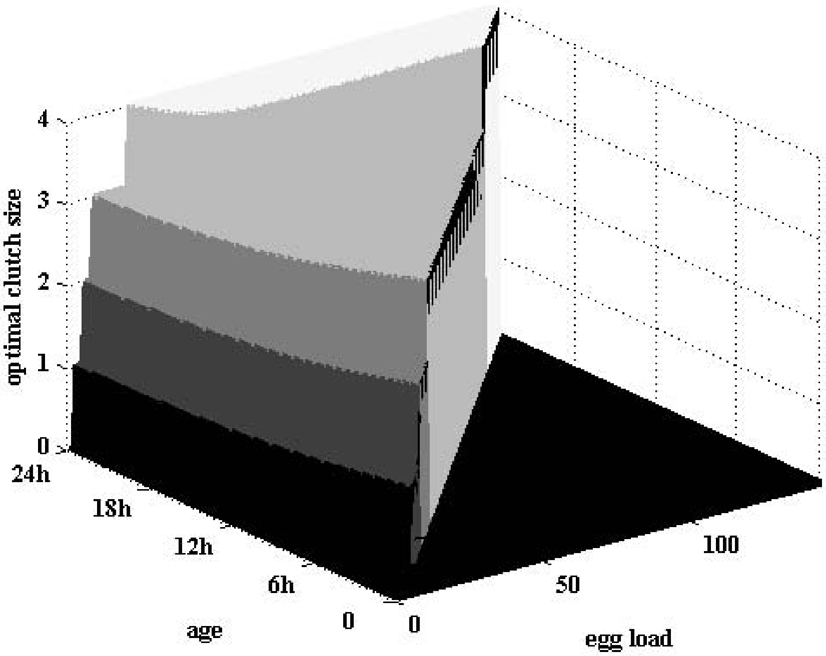

Figure 6: The optimal clutch size from attacks on non-target hosts by synovigenic parasitoids as a function of egg load and age.

take, only one egg can be laid in each host. The only decision, thus, is to accept or to reject it. The new feature of this problem is that there are several classes of hosts, *e.g.*, size classes, and in each class there are several types of hosts, *e.g.*, different instars of different species with the same size. The classes need not be disjoint, but their union must be the whole set Ω of types. This is because, while every type belongs to at least one class, some may have varying characteristcs among individuals that make it possible to belong to one class or another. The parasitoid is assumed to be unable to discriminate the types within the class of a host it encounters. Yet, the expected fitness gained from laying an egg in a host of a given class may vary widely across types within the class.

We may notice that the comparison strategy proposed in subsection 2.1.5 is of this nature. It amounts to have a single class of hosts for both target and non target hosts.

2.3.1 The model

We use similar variables and notations as previously, with the following differences.

- Let Ω denote the (finite) set of possible types.
- There are n classes of hosts, which are subsets Ω_i of the set Ω of types.
- The probability of encountering a host of class i is λ_i,
- The probability of a host of class i being of type ω is $\mu_i(\omega)$, with $\mu_i(\omega) > 0$ if and only if $\omega \in \Omega_i$.
- The fitness gain expected from laying an egg $f(\omega)$ only depends on the host type ω.

The variables t, x, h (now fixed), and T are as previously, as well as the life probability $P(t)$, the conditional probability $\rho(t,\tau) = P(t+\tau)/P(t)$ of surviving from time t to time $t+\tau$, and

$$g(\omega, t) = f(\omega)\rho(t, h)$$

the conditional expected fitness gain of deciding to lay an egg, taking into account the possibility that the parasitoid dies before finishing its oviposition.

We let $G_i(t,x)$ be the expected future fitness gain when attacking a host of class i at time t with an egg complement of x. The dynamic programming equation is now

$$G_i(t,x) = \max\Big\{\sum_{j=1}^{n}\lambda_j \mathbb{E}_T G_j(t+T,x)\,,\\ \sum_{\omega\in\Omega_i}\mu_i(\omega)P(t)g(\omega,t) + \sum_{j=1}^{n}\lambda_j \mathbb{E}_T G_j(t+h+T,x-1)\Big\}\,.$$

This form clearly displays the fact that the optimal policy, *i.e.* reject the host if the first term in the $\max$ operation is larger, accept it if the second term is larger, depends on the class i of the host, but not on its precise type ω.

As previously, it is possible, and may be advisable, to use the conditional expected gain $F_i(t,x) = G_i(t,x)/P(t)$ instead of $G_i(t,x)$. Moreover, introducing the expected return function $F(t,x) = \sum_i \lambda_i F_i(t,x)$, we easily derive from the above that it satisfies

$$F(t,x) = \sum_{i=1}^{n}\lambda_i \max\Big\{\mathbb{E}_T\rho(t,T)F(t+T,x)\,,\\ \sum_{\omega}\mu_i(\omega)g(\omega,t) + \mathbb{E}_T\rho(t,h+T)G(t+h+T,x-1)\Big\}. \tag{11}$$

Again, for each class i, the optimum decision is to lay an egg if the second term in the $\max$ operation is larger. We see that, not unexpectedly, the only class dependent term in these equations is the expected utility of deciding to lay an egg knowing the class i of the host, $\sum_\omega \mu_i(\omega)g(\omega,t)$.

The derivation of Howard's algorithm to numerically solve that equation and its convergence proof goes as in the preceding section. The graphics of figures 5 and 6 show results of a special case of that theory, with only one size class.

3 Final remarks

Parasitoids are complex organisms that display a great deal of adaptive plasticity to circumstances (Godfray 1994). In many cases those circumstances or conditions are state dependent. In this chapter we have shown that this plasticity can be predicted by way of dynamic programming models. How might we use such a tool when working with parasitoids? When it comes to their use in biological control, the key is to elucidate the aforementioned plasticity of individual insects in light of their effects at the population or community level (e.g. impact of parasitoid clutch size on pest population dynamics – Heimpel 2000). This scaling up from the individual to the population level is made more difficult by the extraordinary range of behaviors that parasitoids can display. However the task is manageable if the individual behaviors can be assembled into a kind of policy that is embedded within population-level models (e.g. Mangel and Roitberg 1992). Roitberg (2007) provides a list of parasitoid-based state-dependent opportunities for applied behavioral ecologists working in agricultural settings that range from mass production of parasitoids to pre-release conditioning.

We close by issuing a plea for theoreticians and experimental lab and field parasitoid biologists to work together on parasitoids. Our models clearly show that parasitoid behavior can be greatly affected by physiological constraints and environmental conditions thus the utility for such models in biological control relies on a good understanding of those constraints and conditions. Likewise our models point to novel experiments and approaches for experimental biologists that might otherwise be ignored.

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References

Bigler, F., D Babendreier, D. and Kuhlmann, U. (eds.) (2006). Environmental impact of invertebrates for biological control of arthropods: Methods and Risk Assessment. CABI Press, London.

Bellman, R. (1957) Dynamic Programming. Princeton University Press, Princeton, NJ.

Charnov E.L.: Optimal foraging: the marginal value theorem. Theoretical Population Biology, 9:129–136, 1976.

Clark, C. and Mangel, M. (2000) Dynamic state variable models in ecology: methods and applications. Oxford University Press, New York.

Collier, T. (1995) Adding physiological realism to dynamic state variable models of parasitoid host feeding. Evolutionary Ecology, 9: 217–235.

Desouhant, E, Driessen, G, Amat, I and Bernstein, C. (2005) Host and food searching in a parasitic wasp *Venturia canescens*: a trade-off between current and future reproduction? Animal Behaviour 70: 145–152.

Ellers, J, Sevenster, J, & Driessen, G. (2000). Egg load evolution in parasitoids. The American Naturalist 156, 650-665.

Gerling, D., B.D. Roitberg and M. Mackauer. (1990) Host, instar related oviposition rates in *Aphelinus howardi.* Journal of Insect Behaviour 3: 501–514.

Godfray, H.C.J. (1994) Parasitoids: Behavioral and Evolutionary Ecology. Princeton University Press, Princeton, N.J.

Heimpel, G. (2000) Effects of parasitoid clutch size on host-parasitoid population dynamics. IN (Ives and Hochberg, ed.) Parasite Population Biology, Princeton Univ. Press, Princeton, N.J.

Henry, L., Gillespie, D. and Roitberg, B. (2005) Does other always know best? Oviposition decisions in a parasitoid wasp. Entomol. exp. Appl. 116: 167–174

Henry, L., Roitberg, B. and Gillespie, D. (2006) Covariance of phenotypically plastic traits induces an adaptive shift in host selection behaviour. Proceedings of the Royal Society of London, B. 273: 2893–2899

Hoffmeister, T., Roitberg, B. and Vet, L. (2005) Evolution of solitary parsitoids: a spatially dependent life history approach. The American Naturalist 166: E62–E74.

Houston, A., Clark, C., McNamara, J. and Mangel. (1988) Dynamic models in behavioral and evolutionary ecology. Nature 332: 29–34.

Houston, A. and McNamara, J. (1999) Models of Adaptive Behaviour. Cambridge University Press, Cambridge.

Louda, S.M., Pemberton, R.W., Johnson, M.T. and Follett, P.A. (2003) Nontarget effects —the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annual Review of Entomology 48, 365–396.

Lynch, L.D. and Ives, A.R. (1999) The use of population models in informing nontarget risk assessment in biocontrol. Aspects of Applied Biology 53, 181–188.

Lynch, L.D., Ives, A.R., Waage, J.K., Hochberg, M.E. and Thomas, M.B. 2002. The risks of biocontrol: transient impacts and minimum nontarget densities. Ecological Applications 12, 1872–1882.

Mangel, M. (1989) Evolution of host selection in parasitoids- does the state of the parasitoid matter? American Naturalist 133: 688–705.

Mangel, M. (1989) An evolutionary interpretation of the motivation to oviposit. Journal of Evolutionary Biology 2: 157–172.

Mangel, M. and Roitberg, B. (1992) Behavioural stabilitization of parasite-host dynamics. Theoretical Population Biology 42: 308–320.

Messing, R, Roitberg, B and Brodeur, J. (2006) Measuring and predicting indirect impacts of biological control: Competition, displacement, and secondary interactions. IN (F Bigler, D Babendreier, U Kuhlmann) Non Target Effects of BioControl, CABI Press.

Roitberg, B.D. (1989) The cost of reproduction in rosehip flies: eggs are time. Evolutionary Ecology 3: 183–188

Roitberg, B.D. (2007) Why pest management needs behavioral ecology and vice versa. Journal of Entomological Research (In Press).

Roitberg, B and Mangel, M. (1997) Individuals on the landscape: behavior can mitigate differences among habitats. Oikos 80: 234–240.

Roitberg, B., Sircom, J., Roitberg, C., Alphen, J. and Mangel, M. (1993) Life expectancy and reproduction. Nature 364:18

Roitberg, B. (2000) Threats, Flies and Protocol Gapes: Can behavioral ecology save biological control? Peer reviewed chapter IN (Ives and Hochberg, ed.) Parasite Population Biology, Princeton Univ. Press, Princeton, N.J.

Roitberg, B., Boivin, G. and Vet, L. (2001) Fitness, parasitoids and biological control: an opinion. Canadian Entomologist 133: 429–438.

Rosenheim, J.A. (2000) Characterizing the cost of oviposition in insects: a dynamic model. Evolutionary Ecology 13 : 141–165.

Sirot, E, Ploye, H and Bernstein, C. (1997) State dependent superparasitism in a solitary parasitoid: Egg load and survival. Behavioural Ecology 8: 226–32.

Ueno, T. (1999) Host-feeding and acceptance by a parasitic wasp (*Hymenoptera: Ichneumonidae*) as influenced by egg load and experience in a patch. Evolutionary Ecology 13: 33–44.

Vinson, S.B. and Iwantsch, G. (1980) Host suitability for insect parasitoids. Annual Review of Entomology 25: 397–419

Wajnberg, E. (2006) Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioral mechanisms. Behavioral Ecology and Sociobiology, 60: 589–611.

Wajnberg, E., Bernhard, P. Hamelin, F. and Boivin, G., (2006) Optimal patch time allocation for time limited foragers. Behavioral Ecology and Sociobiology, 60: 1–10.

Wang, X. and Messing, R. (2004) Fitness consequences of body-size-dependent host species selection in a generalist ectoparasitoid. Behavioral Ecology and Sociobiology 56: 513–522

5 Appendix

5.1 Proof of theorem 1

We work with equation (4) and algorithm (7). By its very definition, F is a bounded function. We view equation (4) as a fixed point equation in the space C^0 of bounded continous functions, and algorithm (7) as a Picard sequence for this equation. Items 1 and 3 of the theorem will therefore be a consequence of Banach's fixed point theorem, if we can prove that the r.h.s. of (4) is a contraction in a norm for which C^0 is complete. As is classical, we choose the norm of the uniform convergence: $\|F\| = \sup_{(t,x)\in\mathbb{R}_+^2} |F(t,x)|$. Item 2 is then a consequence of Dynamic programming theory.

We are left with the task of proving that the application $F \mapsto \mathcal{K}(F)$ with

$$\mathcal{K}(F)(t,x) = \mathbb{E}_\omega \max_{c\le x}[\mathbb{E}_T \rho(t, T+h(c))F(t+T+h(c), x-c) + g(\omega,t,c)]$$

is a contraction in C^0. Let also

$$\mathcal{H}(F)(\omega,t,x,c) = \mathbb{E}_T \rho(t, T+h(c))F(t+T+h(c), x-c) + g(\omega,t,c)\,.$$

Let therefore V and W be two bounded continuous functions. We seek a uniform bound to

$$\Delta(t,x) = |\mathcal{K}(V)(t,x) - \mathcal{K}(W)(t,x)|\,.$$

We have

$$\begin{aligned}\Delta(t,x) &= |\mathbb{E}_\omega \max_c \mathcal{H}(V)(\omega,t,x,c) - \mathbb{E}_\omega \max_c \mathcal{H}(W)(\omega,t,x,c)| \\ &\le \mathbb{E}_\omega |\max_c \mathcal{H}(V)(\omega,t,x,c) - \max_c \mathcal{H}(W)(\omega,t,x,c)|\,.\end{aligned}$$

For any two bounded continuous functions $v(c)$ and $w(c)$, it always holds that $|\max_c v(c) - \max_c w(c)| \le \max_c |v(c) - w(c)|$. Using this and the monotonicity of the mathematical expectation operator, and then the monotonicity of the $\max$

operator, we get

$$\begin{aligned}\Delta(t,x) \quad &\le \mathbb{E}_\omega \max\nolimits_c |\mathcal{H}(V)(\omega,t,x,c) - \mathcal{H}(W)(\omega,t,x,c)| \\ &= \mathbb{E}_\omega \max\nolimits_c |\mathbb{E}_T \rho(t, T+h(c)) V(t+T+h(c), x-c) - \\ &\qquad\qquad \mathbb{E}_T \rho(t,T+h(c)) W(t+T+h(c), x-c)| \\ &\le \mathbb{E}_\omega \max\nolimits_c \mathbb{E}_T \rho(t,T+h(c)) |V(t+T+h(c),x-c) - \\ &\qquad\qquad\qquad\qquad W(t+T+h(c), x-c)|\,.\end{aligned}$$

We have $T + h(c) \ge T \ge T_0$ almost surely, by hypothesis, and therefore, almost surely, $\rho(t, T+h(c)) \le \rho(t+T_0) \le r$. By definition of the norm we have endowed C^0 with, $|V(t+T+h(c), x-c) - W(t+T+h(c), x-c)| \le \|V - W\|$. Hence we end up with $\Delta(t,x) \le r\|V-W\|$, and taking the supremum in (t,x)

$$\|\mathcal{K}(V) - \mathcal{K}(W)\| \le r\|V-W\|\,,$$

showing that $\mathcal{K}$ is indeed a contraction, and the theorem is proved.

5.2 Proof of theorem 2

We assume now that for $t \ge L$, $P(t) = 0$, and also that $T \ge T_0 > 0$ almost surely. We have rather work with the recursion for G: $G^0(t,x) = 0$,

$$G^n(t,x) = \mathbb{E}_\omega \max_{c \le x} [\mathbb{E}_T G^{n-1}(t+T+h(c), x-c) + P(t)g(\omega,t,c)]\,.$$

Substitute for G^{n-1} in the r.h.s. in terms of G^{n-2} using the same recursion. This yields

$$\begin{aligned} G^n(t,x) = \quad & \mathbb{E}_{\omega_1} \max_{c_1 \le x} \Bigg\{ P(t) g(\omega_1, t, c_1) + \\ & \mathbb{E}_{T_1} \mathbb{E}_{\omega_2} \max_{c_2 \le x - c_1} \Big[P(t+T_1+h(c_1)) g(\omega_2, t+T_1+h(c_1), c_2) + \\ & \mathbb{E}_{T_2} G^{n-2}(t+T_1+T_2+h(c_1)+h(c_2), x-c_1-c_2) \Big] \Bigg\}\,. \end{aligned}$$

We introduce the notation, for all integer k,

$$\theta_k = t + \sum_{i=1}^{k} (T_i + h(c_i))$$

and carry out this substitution recursively for ℓ steps, to get

$$\begin{aligned} G^n(t,x) = \;& \mathbb{E}_{\omega_1} \max_{c_1 \le x} \Bigg\{ P(t) g(\omega_1, t, c_1) + \\ & \mathbb{E}_{T_1} \mathbb{E}_{\omega_2} \max_{c_2 \le x - c_1} \Big[P(\theta_1) g(\omega_2, \theta_1, c_2) + \\ & \mathbb{E}_{T_2} \mathbb{E}_{\omega_3} \max_{c_3 \le x - c_1 - c_2} \Big(P(\theta_2) g(\omega_3, \theta_2, c_3) + \\ & \vdots \\ & \mathbb{E}_{T_{\ell-1}} \mathbb{E}_{\omega_\ell} \max_{c_\ell \le x - \sum_{k=1}^{\ell-1} c_k} [P(\theta_{\ell-1}) g(\omega_\ell, \theta_{\ell-1}, c_\ell) + \\ & \mathbb{E}_{T_\ell} G^{n-\ell}(\theta_\ell, x - c_1 - \ldots - c_\ell)] \ldots \Big) \Big] \Bigg\} . \end{aligned}$$

It follows from the hypothesis that $T \ge T_0$ almost surely that we may restrict the expectations with respect to T to $T \ge T_0$. But then, for ℓ such that $\ell T_0 \ge L$, both

$$P(t + T_1 + \ldots + T_\ell + h(c_1) + \ldots + h(c_\ell)) = 0$$

and thus

$$G^{n-\ell}(t + T_1 + \ldots + T_\ell + h(c_1) + \ldots + h(c_\ell), x - c_1 - \ldots - c_\ell) = 0,$$

so that the above expression can be written without its last term. But then, the r.h.s is independent from n, showing that the recursion reaches a steady state in no more than ℓ steps. The solution of the dynamic programming equation is therefore

$$\begin{aligned} G(t,x) = \;& \mathbb{E}_{\omega_1} \max_{c_1 \le x} \Bigg\{ P(t) g(\omega_1, t, c_1) + \\ & \mathbb{E}_{T_1} \mathbb{E}_{\omega_2} \max_{c_2 \le x - c_1} \Big[P(\theta_1) g(\omega_2, \theta_1, c_2) + \\ & \mathbb{E}_{T_2} \mathbb{E}_{\omega_3} \max_{c_3 \le x - c_1 - c_2} \Big(P(\theta_2) g(\omega_3, \theta_2, c_3) + \\ & \vdots \\ & \mathbb{E}_{T_{\ell-1}} \mathbb{E}_{\omega_\ell} \max_{c_\ell \le x - \sum_{k=1}^{\ell-1} c_k} [P(\theta_{\ell-1}) g(\omega_\ell, \theta_{\ell-1}, c_\ell)] \ldots \Big) \Big] \Bigg\} . \end{aligned}$$

Although not needed, it may be a useful exercize to place this back in the r.h.s. of equation (2), and check that, upon shifting all mute indices by one, we recover identically the same expression.

This shows the theorem, except for the uniqueness of the solution of (2). This uniqueness follows from the remark that, using $\rho(t, t + T_0) < 1$ suffices to show that the mapping $\mathcal{K}$ of the previous proof still satisfies a weak contraction property: for all V, W in C^0, $\|\mathcal{K}(V) - \mathcal{K}(W)\| < \|V - W\|$, which suffices to get the uniqueness (if not the existence) of the fixed point.