Descriptions of superparasitism by optimal foraging theory, evolutionarily stable strategies and quantitative genetics

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Summary

Many parasitoids superparasitize, in which an insect attacks a previously parasitized host, laying an egg in the host even though only one offspring will emerge from the host. In this paper superparasitism is considered from the perspectives of optimal foraging theory, evolutionarily stable strategies, and quantitative genetics. The focal question is: at what point in its life should an individual parasitoid begin attacking previously parasitized hosts? Each of the three theoretical methods can be used to answer the question and by doing so, we see how the three methods are connected. Qualitative, empirical predictions based on the theories are described.

Keywords: superparasitism; optimal foraging theory; evolutionarily stable strategies; quantitative genetics; evolution in function space

Introduction

Two theoretical methods commonly used in behavioural studies are Optimal Foraging Theory (OFT) and the theory of Evolutionarily Stable Strategies (ESS). They are focused, more or less, on the individual with the aim of predicting the behaviour of individuals. A third theoretical method is the theory of Quantitative Genetics (QG), which attempts to predict the evolution of behaviour in populations. Although most practitioners employ only one type of approach, there is usually fervent belief that the approach used is the best (if not the only) one to use. Rarely have the three methods been compared for the same problem (see Rosenzweig *et al.*, 1987, for discussion). Charlesworth (1990) recently compared an optimization approach for population growth with a QG approach. However, that comparison did not consider individual behaviour.

In this paper, a particular biological problem is considered from the perspective of these three theories. The biological phenomenon of *superparasitism* comprises an insect laying an egg in a previously parasitized host, from which only one offspring will emerge. By developing OFT, ESS and QG theories of superparasitism, one is able to understand when the three methods will give the same result and when and why the predictions will diverge. Over a wide range of assumptions and parameter values, it appears that the three theories give consonant predictions. This study also shows how evolutionary ecology and population genetics are linked. Population genetics asks, 'What does evolution do, once the fitness function is given?'; and evolutionary ecology asks, 'How do ecology and behaviour determine the fitness function?'. In general, we must consider both kinds of questions; by linking behavioural ecology and quantitative genetics, we can make both fields stronger.
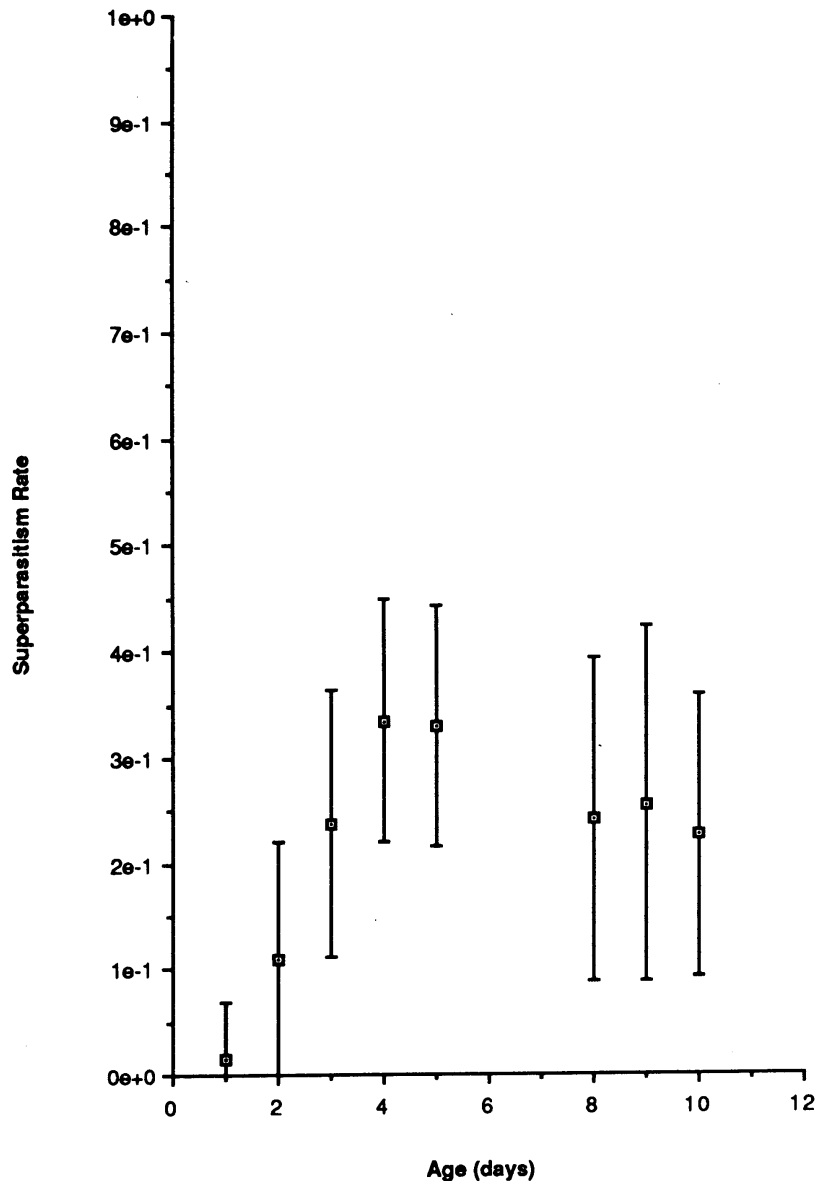
Figure 1. Rate of superparasitism by the parasitoid *Ephredrus californicus* (Baker) attacking pea aphids. Redrawn from Voelkl and Mackauer (1990).

The phenomenon

After oviposition, an insect may leave a chemical trail on the host. Such behaviour is found in parasitoids, tephritid fruit flies, and many herbivorous insects. Roitberg and Prokopy (1987) review host marking by herbivorous insects of three orders (Coleoptera, Diptera and Lepidoptera). In many cases, particularly involving parasitoids and tephritid fruit flies, only one offspring will emerge from a host (insect larvae or fruit), yet on occasion we observe oviposition in a previously parasitized and marked host. This phenomenon is called *superparasitism* or *superoviposition*. For many years, it was thought that superparasitism was a 'mistake' by the ovipositing insect. In the early 1980s a number of investigators recognized that superparasitism can be an adaptive strategy in the sense that by ovipositing in a previously parasitized host a

female achieves higher expected lifetime reproduction than by rejecting such a host (reviewed in Mangel and Clark, 1988, Chapter 4; and van Alphen and Visser, 1990). The propensity to superparasitize changes over the course of an insect's lifetime. For example, Fig. 1 shows the rate of superparasitism (Voelkl and Mackauer, 1990) by a wasp that attacks aphids. The propensity to superparasitize also depends upon the ecological and social conditions surrounding the parasitoid (Visser *et al.*, 1990). If superparasitism is, in fact, an adaptive strategy (van Alphen and Visser, 1990), then we should be able to assess the selection acting on it, either alone or in conjunction with other behavioural traits.

van Alphen and Visser (1990) review superparasitism as an adaptive strategy and develop a model based on rate maximization to study selection on superparasitism. They model two strategies (defend a patch and never superparasitize versus allow conspecifics to enter the patch and superparasitize); it is possible, of course, that other strategies also exist. A number of authors have concluded that because superparasitism clearly involves the behaviour of other individuals (van Alphen and Vet, 1986, pp. 37ff), one must use methods of game theory to analyse superparasitism. Hubbard *et al.* (1987) provide one such example in which a simulation based on the assumption of rate maximization is used to assess the fitness consequences and avoidance of superparasitism.

van Alphen (1988) reviews the state of analysis of superparasitism and concludes, 'Because optimal patch times are dependent on the patch times that other parasitoids are willing to invest, patch-time allocation and superparasitism should be analysed with an ESS rather than with an optimal foraging approach' (pp. 220). One objective of this paper is to ask when the *behaviours* predicted by different theories would be the same. To do this, the theory of superparasitism is developed from three perspectives: (1) the theory of optimal foraging; (2) the theory of evolutionarily stable strategies; and (3) the theory of quantitative genetics. By doing this, we are able to ascertain when the three approaches will give similar predictions of behaviour and when they will not, and why the predictions are similar or differ. Charlesworth (1990) performed an analysis in a similar spirit, but concentrated on population parameters. Here the focus is individual behaviour.

General assumptions

The following assumptions are common to all analyses:

1. The measure of fitness the expected number of offspring accumulated by the insect through ovipositions over the course of its life.
2. The parasitoid is solitary: only one offspring will emerge from a host, regardless of the number of eggs laid in it.
3. The parasitoid is univoltine and all individuals emerge more or less synchronously.
4. Lifetime fitness is assessed at time T, which is fixed. Time before T is measured discretely in unit intervals called periods. (In the Appendix, a continuous time model is developed.)
5. The parasitoid is not egg limited, so that one can ignore egg load as a state variable (Mangel and Clark, 1988). This would occur if the parasitoid produces eggs throughout its life or emerges with an egg complement that vastly exceeds expected reproductive opportunities.
6. There is a 'somatic cost of reproduction' in the sense that survival during a period in which oviposition occurs is lower than survival during a period in which oviposition does not occur. Supporting evidence can be found in Roitberg (1989). Handling time is sufficiently short that the only cost for oviposition is the survival cost.
7. Marking of the host and detection of the mark by the parasitoid are perfect. Alternatives are discussed in Roitberg and Mangel (1988).

8. There are two host types. Host type 1 is previously unparasitized and yields, on average, f_1 offspring per egg. Host type 2 is previously parasitized and yields, on average, f_2 offspring per egg. Here $f_2 < f_1$. The computation of f_2 includes an average of eggs in a previously parasitized host.

Optimal foraging: games against nature

The theory of optimal foraging can be viewed as a game against nature, in which the parasitoid's actions might change the environment, but one does not consider the strategies of conspecifics. The simplest case is one in which the parasitoid moves through a world of patches, in which only one parasitoid visits a patch at a time. Thus when an individual encounters a patch, it already contains a mixture of unparasitized and previously parasitized hosts. By assuming that the number of hosts is very large, we can ignore depletion of unparasitized hosts by a single parasitoid. This also means that the likelihood of self-superparasitism (cf. Visser *et al.*, 1990) can be ignored. Theoretical alternatives are discussed by Roitberg and Mangel (1988) and Visser *et al.* (1990). Introduce the following probabilities:

Prob{encounter a host type i in a single period} = λ_i
Prob{parasitoid survives a single period, given no oviposition} = $e^{-\mu}$
Prob{parasitoid survives a single period, given oviposition} = $e^{-\gamma\mu}$ (1)

The parametrization of survival as an exponential is chosen to be consistent with the continuous time model developed in the Appendix and $\gamma > 1$ is a measure of the survival cost of oviposition. For example, γ could involve increased handling time during oviposition (Mangel, 1989).

Lifetime fitness is defined as:

$F(t)$ = Maximum expected reproduction from ovipositions between t and T   (2)

where the maximum is taken over oviposition decisions (i.e. to oviposit or not) in hosts encountered between t and T. The time T plays the role of a terminal time, at which point $F(T) = 0$.

It is easy to show that if an unparasitized host is encountered, then the parasitoid should always oviposit. Lifetime fitness $F(t)$ satisfies an equation of dynamic programming (Mangel and Clark, 1988) given by:

$$
\begin{aligned}
F(t) = &\ (1 - \lambda_1 - \lambda_2)\ e^{-\mu}\ F(t+1) \\
&+ \lambda_1\ \{f_1 + e^{-\gamma\mu}\ F(t+1)\ \} \\
&+ \lambda_2\ \max\{f_2 + e^{-\gamma\mu}\ F(t+1);\ e^{-\mu}\ F(t+1)\}
\end{aligned}
\tag{3}
$$

The three terms on the right-hand side of Equation 3 correspond to the mutually exclusive events of Equation 1 not encountering a host of either type during period t, Equation 2 encountering a host of type 1 during period t or Equation 3 encountering a host of type 2 during period t. If a host of type 2 is encountered, then the parasitoid oviposits or not according to the behaviour that gives higher fitness. A more general form of Equation 3 would allow the parasitoid a probability of ovipositing in a previously parasitized host. It can be shown that expected lifetime reproduction is maximized when this probability is either 0 or 1; this leads to Equation 3.

The solution of Equation 3 gives a time t_s that determines a behavioural change. In particular, if $t < t_s$ then whenever a host of type 2 is encountered, it should be rejected. When $t > t_s$, then whenever a host of type 2 is encountered, it should be accepted for oviposition. This time is determined during the numerical solution of Equation 3; it may be that $t_s > T$ (i.e. never accept a host of type 2) or that $t_s = 0$ (always accept a host of type 2). An analytical description of t_s can be

found in the following manner. In the interval $[t_s, T]$, Equation 3 becomes:

$$
\begin{aligned}
F(t) &= (1- \lambda_1 - \lambda_2)\, e^{-\mu}\, F(t+1) + \lambda_1\, \{f_1 + e^{-\gamma\mu}\, F(t+1)\} \\
&\quad + \lambda_2\, \{f_2 + e^{-\gamma\mu}\, F(t+1)\} \\
&= [e^{-\mu} + (\lambda_1 + \lambda_2)(e^{-\gamma\mu} - e^{-\mu})]\, F(t+1) \\
&\quad + \lambda_1 f_1 + \lambda_2 f_2
\end{aligned}
\tag{4}
$$

Defining the time to go $s = T - t$, Equation 4 can be written as:

$$
F(s+1) = A + BF(s)
\tag{5}
$$

with the initial condition $F(0) = 0$. The solution of this linear difference equation is:

$$
F(s) = A \sum_{j=0}^{s-1} B^j
\tag{6}
$$

In the interval $[0, t_s-1]$, Equation 3 becomes:

$$
\begin{aligned}
F(t) &= (1- \lambda_1 - \lambda_2)\, e^{-\mu}\, F(t+1) + \lambda_1\, \{f_1 + e^{-\gamma\mu}\, F(t+1)\} \\
&\quad + \lambda_2\, e^{-\mu}\, F(t+1) \\
&= [e^{-\mu} + \lambda_1(e^{-\gamma\mu} - e^{-\mu})]\, F(t+1) + \lambda_1 f_1
\end{aligned}
\tag{7}
$$

which can be written in terms of the time to go as:

$$
F(s + 1) = A' + B'F(s)
\tag{8}
$$

Note that $B' > B$ but $A' < A$. If s^* corresponds to the time t_s, at which point

$$
F(T-s^*) = A \sum_{j=0}^{T-s^*-1} B^j ,
$$

the solution of Equation 8 is:

$$
F(s + s^*) = A' \sum_{j=0}^{s-1} (B')^j + (B')^s\, F(T - s^*)
\tag{9}
$$

with the understanding that $s \geq 1$. The optimal time for the behavioural change, t_s, is then computed from the condition described by the 'max' in Equation 3. As is evident from the equations, the time t_s computed in this manner will, in principle, be a function of the encounter rates, the fitnesses, and the survival parameters γ and μ.

An analogue of Equation 3 can be used to determine a 'fitness surface' associated with all switching times that run between $t = 1$ and $t = T$ (Fig. 2). To do this, we specify a particular value of the switching time t_s and then solve an equation similar to Equation 3 with the term associated with previously parasitized hosts determined by whether $t > t_s$ or not (rather than through a maximization). At any particular value of encounter rates (e.g. Fig. 2a) there is an optimal switching time, although times close to optimal have fitness that is nearly the same as optimal. In addition, when many values of encounter rates are compared (Fig. 2b), the fitness surfaces are relatively flat for low values of encounter rates. Note too that there is an asymmetry in the fitness curves: the fitness associated with values of t_s larger than optimal is generally higher than values of t_s smaller than optimal (but the same difference from optimal). On the empirical side, we predict that individuals which are not acting 'optimally' would be more likely to superparasitize later, rather than earlier.
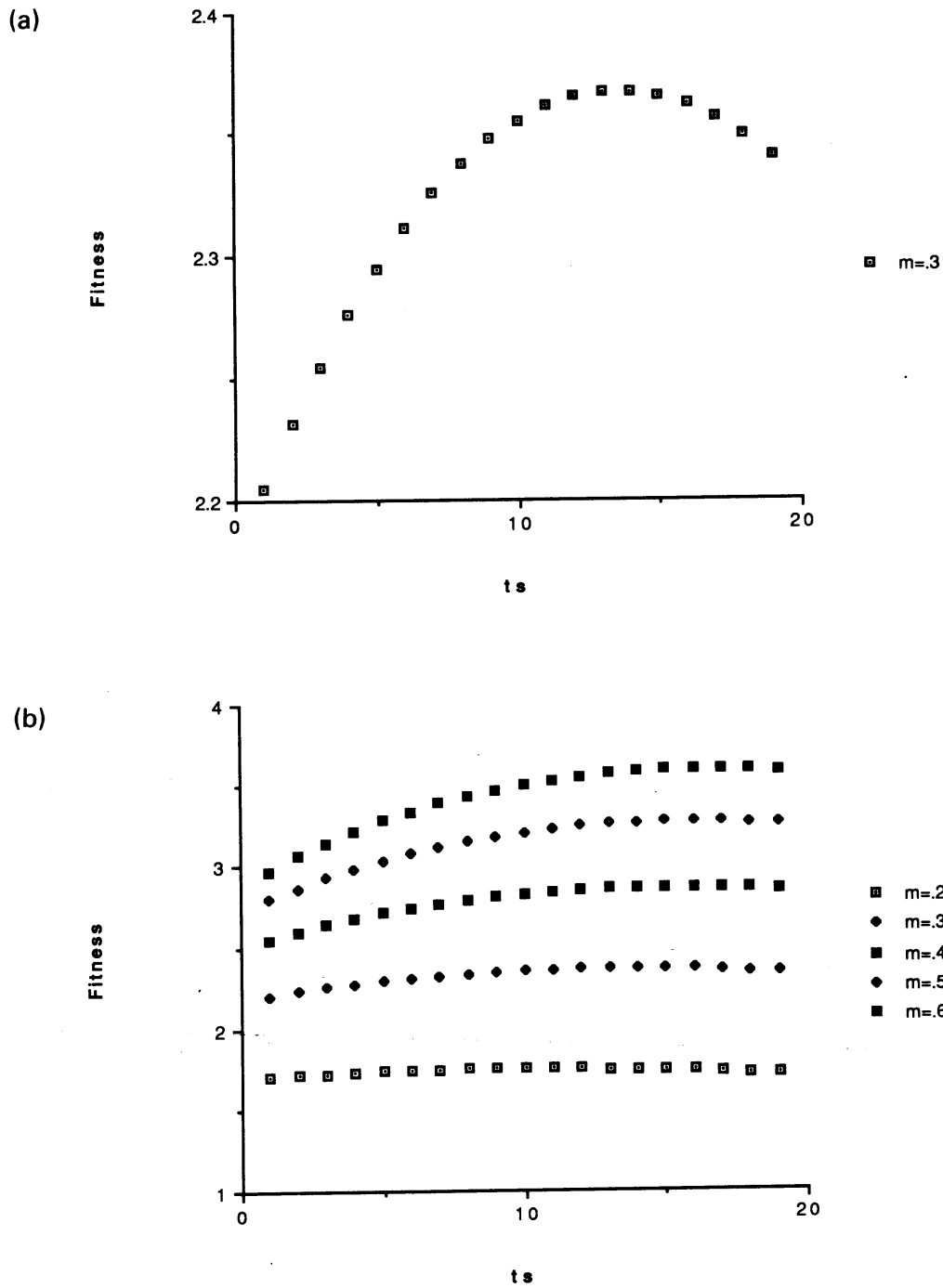
(a)

(b)

Figure 2. Fitness surface associated with different values of the switching time. An analogue of Equation 3 was solved (described in the text) to determine the fitness surface. Here $\lambda_1 = 0.6\,m$, $\lambda_2 = 0.4\,m$ where m is a parameter ranging from 0 to 1. In addition, $f_1 = 1$, $f_2 = 0.2$, $e^{-\mu} = 0.99$, $e^{-\gamma\mu} = 0.795$ and T = 20. (a) The fitness surface for $m = 0.3$. (b) The fitness surface for a range of values of m.

Evolutionarily stable strategies: games against conspecifics

The basis of an ESS approach to superparasitism is that conspecifics in a patch may affect the behaviour of other individuals because the conspecifics affect the environment experienced by other individuals. To begin then, we must model how conspecifics affect the environment. Following the usual ESS terminology, refer to the conspecifics as the 'normal' parasitoids and the distinguished individual as the 'mutant' parasitoid.

Conspecifics change the environment of the mutant by modifying the number of unparasitized and parasitized hosts. Thus let:

$N_u(t)$ = number of unparasitized hosts at the start of period t

$N_p(t)$ = number of parasitized hosts at the start of period t (10)

Since hosts are conserved, $N_u(t) + N_p(t) = N_0$, a constant. Next, let $P(t)$ denote the number of normal parasitoids alive at the start of period t and let t^* (which is what we are trying to find) denote the time at which normal individuals begin ovipositing in previously parasitized hosts.

In order to construct the dynamics of $N_u(t)$ and $P(t)$, we must model the searching by parasitoids for hosts. Searching can be characterized by a search parameter ϵ:

Prob{individual parasitoid finds a single host in one period of search} = $1 - e^{-\epsilon}$ (11)

Thus, $1/\epsilon$ is roughly the mean number of periods required for a single parasitoid to find a single host. This can be related (Mangel, 1985) to the search abilities of the parasitoid and the area of the region in which hosts are found. In light of Equation 11, we have:

Prob{a particular host is not found | P parasitoids are searching} = $e^{-\epsilon P}$

Prob{a particular parasitoid finds a host | N hosts are present} = $1 - e^{-\epsilon N}$ (12)

Assuming that parasitoids search independently and that hosts are encountered randomly, the host dynamics become:

$$N_u(t + 1) = N_u(t)\, e^{-\epsilon P(t)}$$
$$N_p(t + 1) = N_0 - N_u(t + 1)$$ (13)

Unlike the case of optimal foraging theory, depletion of unparasitized hosts by the *population* of parasitoids is taken into account by the ESS approach. However, the dynamics still assume that the probability of re-encountering a specific host is essentially 0; this could be modified (Roitberg and Mangel, 1988). The host dynamics now determine time-dependent encounter rates which are:

$$\lambda_1(t; t^*) = (1 - e^{-\epsilon N_0})\frac{N_u(t)}{N_0}$$

$$\lambda_2(t; t^*) = (1 - e^{-\epsilon N_0})\frac{N_p(t)}{N_0}$$ (14)

In each of these equations, the first term, $1 - e^{-\epsilon N_0}$, is the probability that any kind of host is encountered during period t; and the second term, either N_u/N_0 or N_p/N_0, is the conditional probability that a host of a particular type is encountered.

In order to describe the parasitoid dynamics, it helps to use the Heaviside step function, $H(z)$ defined by:

$$H(z) = \begin{cases} 1 & \text{if } z \geq 0 \\ 0 & \text{otherwise} \end{cases} \tag{15}$$

Using this function, the dynamics of the parasitoid population are

$$P(t + 1) = P(t) [(1 - \lambda_1(t; t^*) - \lambda_2(t; t^*)) \, e^{-\mu} + \lambda_1(t; t^*) \, e^{-\gamma\mu}$$
$$+ \lambda_2(t; t^*) \{H(t - t^*) \, e^{-\gamma\mu} + H(t^* - t) \, e^{-\mu}\}] \tag{16}$$

The three terms on the right-hand side of this equation correspond to the mutually exclusive events of not encountering any host during period t, encountering an unparasitized host (in which oviposition always occurs) and encountering a previously parasitized host (in which oviposition occurs if $t \geq t^*$).

By solving Equations 13–16, with initial conditions $N_u(0) = N_{u0}$, $N_p(0) = N_{p0}$ and $P(0) = P_0$, the normal individuals generate an environment for the mutant. This environment is characterized by the encounter rates $\lambda_i(t; t^*)$. We can now extend the definition of lifetime fitness given in Equation 2 to:

$$F(t; t^*) = \text{Maximum expected reproduction of the mutant parasitoid from}$$
$$\text{ovipositions between } t \text{ and T, when the normal parasitoids are}$$
$$\text{characterized by } t^* \tag{17}$$

The maximum in Equation 17 is determined by the switching time t_s that the mutant uses when the normal individuals are using the switching time t^*. The dynamic programming equation for $F(t; t^*)$ is virtually identical with Equation 3:

$$F(t; t^*) = (1 - \lambda_1(t; t^*) - \lambda_2(t; t^*)) \, e^{-\mu} \, F(t + 1; t^*)$$
$$+ \lambda_1(t; t^*) \{f_1 + e^{-\gamma\mu} \, F(t + 1; t^*)\}$$
$$+ \lambda_2(t; t^*) \max\{f_2 + e^{-\gamma\mu} \, F(t + 1; t^*); e^{-\mu} \, F(t + 1; t^*)\} \tag{18}$$

with the same end condition that $F(T; t^*) = 0$. In Equation 18, we assume that the mutant has negligible effect on the dynamics of the environment experienced by the normal individuals.

As before, solution of Equation 18 generates a switching time t_s for the mutant. Since lifetime fitness (expected lifetime reproduction) for the mutant is $F(1; t^*)$, the ESS condition is that $F(1; t^*)$ is maximized when t_s, determined in the solution of Equation 18, equals t^*. Results (Table 1) are easily obtained by numerical solution. From these results, we conclude the following:

Table 1. Comparison of switching behaviours in the OFT and ESS formulations. Parameters are $f_1 = 1$, $f_2 = 0.2$, $e^{-\mu} = 0.99$, $e^{-\gamma\mu} = 0.795$, T = 20

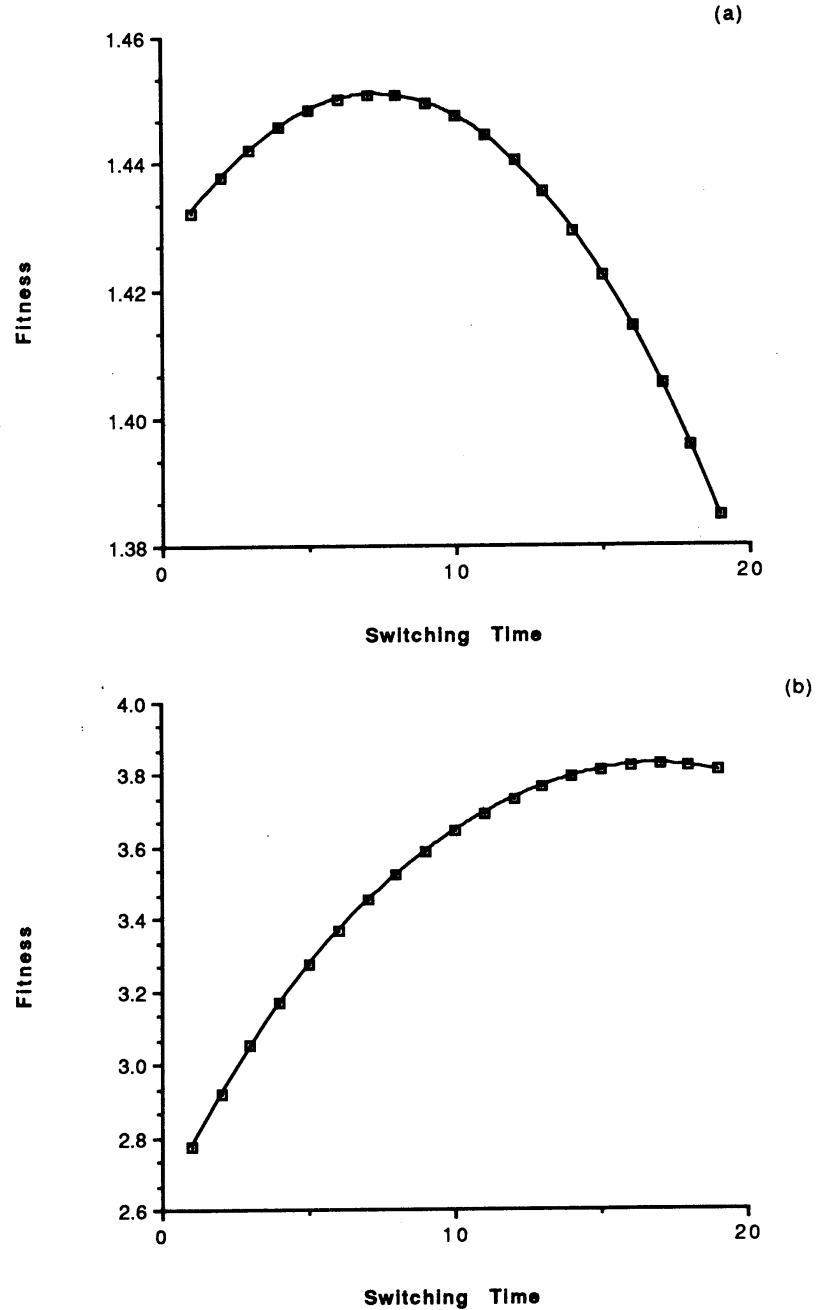| P(0)	$N_u(0)$	$N_p(0)$	t_s	
			OFT	ESS
1	120	80	9	9
10	120	80	9	8
20	120	80	9	7
70	120	80	9	3
70	4200	2800	18	17
50	3000	2000	18	17
20	1200	800	18	17
10	600	400	17	17

Figure 3. Fitness functions depending upon switching time in the ESS theory. In each panel, the fitness for a mutant using each switching time is computed when the population uses the ESS switching time. Parameters as in Table 1, except as follows. (a) Initial number of conspecifics = 20, of unparasitized hosts = 120, of parasitized hosts = 80. (b) Initial number of conspecifics = 70, of unparasitized hosts = 4200, of parasitized hosts = 2800. For (a) the switching time based on OFT is $t_s^* = 9$ while that based on ESS theory is $t_s^* = 7$. For (b) the switching time based on OFT is $t_s^* = 18$ while that based on ESS theory is $t_s^* = 17$. Note that in (a) the range of fitness values is about 1.38 –1.45, suggesting that selection for the optimal value of switching time will be weak. On the other hand, the range in (b) is 2.75–3.8, suggesting that there may be strong selection for switching values larger than 13 or 14.

1. In general the switching time computed by OFT is larger than the switching time computed by ESS theory. From the empirical perspective, we predict that individuals in groups will begin superparasitizing sooner than solitary individuals.

2. Equality holds when the normal parasitoids don't appreciably change the environment experienced by the mutants; roughly when $N_0 \gg P(0)$. Note, however, that in the last four entries in Table 1 the ratio $N_0/P(0)$ is constant but differences in behaviour occur, so it is more than strict inequality of numbers that determines when the OFT and ESS results agree or disagree.

3. When the two results differ, an individual who adopts the OFT result has lower lifetime fitness than the individuals adopting the ESS result (Fig. 3). Note that the differences in fitness for different values of switching time may not be large. This suggests that selection for 'optimal behaviour' may be weak.

4. There are cases in which a pure ESS does not exist. Those are cases in which, given t^*, the fitness of the mutant was maximized at a switching value not equal to t^*. In such a case, a mixed ESS might be possible.

5. Finally, the procedure outlined here is a general procedure for dealing with conspecifics and how they change the environment.

Quantitative genetics: evolution in function space

Recent work (Kirkpatrick, 1988; Kirkpatrick and Heckman, 1989) has laid the foundation for a quantitative genetic theory for the kinds of behavioural problems discussed in this paper. Here, I outline how such a theory could be used to study the evolution of the time at which individuals in a population of parasitoids begin superparasitizing. Certain missing elements prevent as complete a solution as for the case of OFT or ESS.

The theory involves the study of evolution in function spaces (Riesz and Sz.-Nagy, 1978; Yoshida, 1980). Suppose that a parasitoid of a given genetic composition can be characterized by a function $P(t), t = 1, 2, \ldots T - 1$, which is the probability that a previously parasitized host will be accepted for oviposition in period t if it is encountered. The lifetime fitness of such a parasitoid can be computed by the analogue of Equation 3. We let $F\{t| P(s) \ s = t, t + 1, \ldots T - 1\}$ denote the expected reproduction between t and T, for a parasitoid that has behaviour determined by acceptance function $P(s)$. The analogue of Equation 3 is:

$$
\begin{aligned}
F\{t| \ P(s) \ s = t, t + 1, \ldots T - 1\} = \\
(1 - \lambda_1 - \lambda_2) \ e^{-\mu} \ F\{t + 1| P(s) \ s = t + 1, \ldots T - 1\} \\
+ \lambda_1\{f_1 + e^{-\gamma\mu} \ F\{t + 1| P(s) \ s = t + 1, \ldots T - 1\}\} \\
\lambda_2[P(t) \ (f_2 + e^{-\gamma\mu} \ F \ (t + 1 \ | \ P(s) \ s = t + 1, \ldots \\
T - 1) \\
+ (1 - P(t)) \ e^{-\mu} F(t + 1) \ P(s) \ s = t + 1, \ldots \\
T - 1)]
\end{aligned}
\tag{19}
$$

Lifetime fitness is then $F\{1| \ P(s) \ s = 1, 2, \ldots T - 1\}$, computed by backward iteration using Equation 19. For simplicity, I shall write $F\{1| P(s)\}$ or $F\{1| P(t)\}$ for $F\{1| P(s) s = 1, 2, \ldots T - 1\}$

Let Z denote the space of all possible acceptance functions. An example would be:

$$
Z = \text{All continuous functions } P(t) \text{ with } 0 \leq P(t) \leq 1
\tag{20}
$$

Readers who are not familiar with functional analysis might want to simply consider $P(t)$ to be the family of all possible normal cumulative distribution functions, parametrized by the mean and variance of the normal density.

Each function $P(t)$ in the space Z has a fitness associated with it, determined by Equation 19. That is, lifetime fitness is a functional which takes elements of the function space and returns a

real number. We can study selection and evolution in this function space using the following procedure:

1. Start with some 'density' of functions $P(t)$ in the function space Z. For each function compute the fitness determined by Equation 19.
2. Use the fitnesses to renormalize the density of functions in Z.
3. The density of functions in the next generation is determined by the genetic variance–covariance, i.e. the heriditary mechanism.

In general, this procedure would be implemented as follows. We measure the density by a function $M(Z, P(t))$ dP defined so that:

$$M(Z, P\ t))\ dP = \text{fraction of trajectories in } Z \text{ that are within } dP$$
$$\text{of the trajectory } P(t) \qquad (21)$$

The density of functions after selection is then proportional to $M(Z, P(t))F\{1| P(t)\}$, since $F\{1| P(t)\}$ determines the selection on individuals with acceptance function $P(t)$. The mean function after selection $P^*_{av}(t) = E\{P(t)F\{1| P(t)\}\}/E\{F\{1| P(t)\}\}$ is found by averaging in Z using the density of functions $M(Z, P(t))$.

Reproduction occurs after selection. To characterize reproduction we must describe the function $P_{off}(t)$ of the offspring when the parents are characterized by the functions $P_1(t)$ and $P_2(t)$. For example, one choice might be:

$$P_{off}(t) = [P_1(t) + P_2(t)]/2 \qquad (22)$$

In general, we must describe an offspring function $O(P_{off}(t); P_1(t), P_2(t))$; this function contains the genetic variance–covariance. Within this formalism, we are then able to describe the density of trajectories $M(Z', P(t))$ in the next generation. It is:

$$M(Z', P_{off}(t))\ dP_{off} = \iint O(P_{off}(t); P_1(t), P_2(t))\ M'(Z, P_1(t))$$
$$M'(Z, P_2(t))\ dP_1 dP_2 dP_{off} \qquad (23)$$

Here $M'(Z, P_1(\text{t}))$ is the density of trajectories in Z around $P_1(t)$ after selection. To generalize Equation 23, we would have to specify the joint density of parental acceptance functions.

Kirkpatrick (1988), Kirkpatrick and Heckman (1989) and Kirkpatrick *et al.* (1990) have extended the finite dimensional Gaussian theory of quantitative genetics to provide a procedure that makes Equations 19 to 23 a practicable programme. Their procedure involves the following:

1. Assume that the function space is the space of Gaussian processes (Prohorov and Rozanov, 1969). These processes are characterized by a mean and a covariance function C. The covariance matrix is assumed, as in the finite dimensional case, to be composed of genotypic G and environmental B terms such that $C = G + B$
2. Specify the mean function $P_{av}(t)$
3. The mean function after selection $P^*_{av}(t)$ is

$$P^*_{av}(t) = E[P(t)\ F\{1| P(t)\}]/E\ \{F\{1| P'(t)\}\} \qquad (24)$$

where now the averages are taken with respect to the density of Gaussian functions in the function space with mean $P_{av}(t)$ and covariance function C and E denotes the average over this function space. In order to compute $P^*_{av}(t)$, we must know the fitness of functions $P(t)$ and this is where behavioural ecology interfaces with quantitative genetics since behavioural models provide a means for determining the fitness associated with a given acceptance function. To implement Equation 24, one could partition the set of possible functions (either by Monte Carlo

simulation or by a regular search over functions), choose functions from this partition, and average.

4. The selection differential is $S = P^*_{av}(t) - P_{av}(t)$. Note that in order to find the selection differential, one needs to know $P^*_{av}(t)$, which means that the fitness function is needed. As it is usually developed, quantitative genetics treats fitness in an *ad hoc* manner (e.g. the assumption of Gaussian fitness) that is external to the theory. That is, the theory is not self contained if one wants to *predict* behaviours, rather than *estimate* selection, show that mean fitness increases or predicts the evolution of a population mean, given a fitness function.

5. The change in the mean trajectory is then

$$\Delta P_{av}(t) = G\, C^{-1}[P^*_{av}(t) - P_{av}(t)] \tag{25}$$

This procedure can be effectively applied once the functions in Z are decomposed by an eigenfunction expansion (Kirkpatrick and Heckman, 1989).

The objective of the eigenfunction expansion is to be able to write that the mean trajectory in generation n is given by:

$$P_{av}(t,n) = \sum_{i=1}^{\infty} a_i(n)\, \phi_i(t) \tag{26}$$

where the ϕ_i are eigenfunctions associated with the genetic variance–covariance matrix and the coefficients $a_i(n)$ are to be determined. In general, they will satisfy nonlinear difference equations. Once these difference equations for the $a_i(n)$ are determined, we can introduce a measure of how closely the mean population trajectory approximates the optimal individual behaviour. The mean square deviation between the two has theoretical justification and is:

$$D(n) = \int_{0}^{t^*} P_{av}(t,n)^2 dt + \int_{t^*}^{T} (P_{av}(t,n) - 1)^2\, dt \tag{27}$$

We are interested in the question of whether or not evolution can drive the mean function, say, to match closely the solution predicted by OFT or ESS theory. More importantly, however, we should be most interested in the differences in the fitness of the optimal individual behaviour predicted by OFT or ESS theory and the fitness of the behaviour of the QG model. This is especially important from an empirical perspective, since it is the fitness of behaviours and not the actual behaviours themselves that is important for selection. The methods described here allow us to compute the fitness of any superparasitism behaviour.

Discussion

The methods presented here can be generalized. For example, in many cases (Mangel, 1987) egg complement and time are important in the analysis of the oviposition behaviour of an insect that can attack many different hosts. The approach of OFT then leads to a decision matrix $\{d_i^*(x,t)\}$ describing the optimal number of eggs to lay on host type i in period t when the egg complement is x. The generalization of the method in this paper would be, for each host type, a time $t_i^*(x)$, which is the ESS time and egg load at which a host of type i should be accepted for oviposition. The rest of the analysis is similar to that in this paper. Similar extensions could include information states and fecundity.

The procedures described above allow us to compare OFT, ESS and QG models for individual behaviour in a manner similar to the study by Charlesworth (1990) for population properties

Table 2. A comparison of the three methods used for the analysis of superparasitism

	OFT	ESS	OG
Level of the model	Individual	Individual and population	Population
Criterion	Absolute fitness maximization	Relative fitness maximum	Maximization of mean population fitness or no maximization
Selection level	Phenotypic	Phenotypic	Phenotypic translated to genetic
Dynamics/ maintenance of genetic variation	No mechanism provided	No mechanism provided	Possible mechanism depending on model
Genetic model	Haploid one locus	Haploid one or two loci	Many loci
Genetic covariance	No	No	Yes
Constraints on strategies	Explicit	Explicit	Explicit and implicit
Time scale of predictions	Short term	Short term	Long term

(Table 2). The methods developed here also provide a natural way, via Equation 19, to determine the fitness functional for evolution in function space. That is, one need no longer assume that lifetime fitness is normally distributed. The assumption of normality simplifies the analysis of evolution because the treatment of heredity is simplified, but sacrifices biology for this simplification. Behavioural ecology allows us to compute fitnesses associated with behavioural programmes. The interaction of behavioural ecology and quantitative genetics will strengthen each.

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Appendix: The continuous time optimal foraging model

This appendix shows how to formulate and solve the continuous time version of the optimal foraging model. This is done for completeness of the analysis as well as to show that dynamic models of foraging can have analytical solutions; they may not, however, be easy.

To formulate this model, the encounter assumption is:

$$Pr\{\text{encounter host type } i \text{ in the next } dt\}$$
$$= \lambda_i dt + o(dt) \tag{A.1}$$

where $o(dt)$ denotes terms such that $o(dt)/dt \to 0$ as $dt \to 0$. The essence of this assumption is that the λ_i are no longer probabilities, but are now rates. Survival is characterized by

$$Pr\{\text{survive } s \text{ time units into the future | searching}\} = e^{-\mu s}$$
$$Pr\{\text{survive } s \text{ time units into the future | ovipositing}\} = e^{-\gamma \mu s} \tag{A.2}$$

As in the previous optimal foraging model, let $F(t,T)$ denote the maximum expected lifetime fitness accumulated through ovipositions between t and T. If handling time is h, the analogue of Equation 3 is:

$$F(t,T) = (1 - (\lambda_1 + \lambda_2)\, dt)\, e^{-\mu dt}\, F(t+dt,T)$$
$$+ \lambda_1\, dt\, \{f_1 + e^{-\gamma\mu(dt+h)}\, F(t + dt + h,T)\}$$
$$+ \lambda_2\, dt\, \max\{e^{-\mu dt}\, F(t + dt,T);\, f_2 + e^{-\gamma\mu(dt+h)}\, F(t + dt + h,T)\}$$
$$+ o(dt) \tag{A.3}$$

Following the procedure of Taylor expanding in powers of dt, collecting terms according to dt and allowing $dt \to 0$ lead to the differential-difference equation:

$$0 = \frac{\partial F(t,T)}{\partial t} - (\lambda_1 + \lambda_2 + \mu)\, F(t,T) + \lambda_1\{f_1 + e^{-\gamma\mu h}\, F(t+h,T)\}$$

$$+ \lambda_2\, \max\{F(t,T);\, f_2 + e^{-\gamma\mu h}\, F(t + h,T)\} \tag{A.4}$$

with end condition $F(T,T) = 0$.

Once again, there is a time t_s such that when $t > t_s$, it is optimal to accept host type 2. For values of $t > t_s$, then Equation A.4 becomes

$$0 = \frac{\partial F(t,T)}{\partial t} - (\lambda_1 + \lambda_2 + \mu)\, F(t,T) + \lambda_1\{f_1 + e^{-\gamma\mu h}\, F(t+h,T)\}$$

$$+ \lambda_2\, \{f_2 + e^{-\gamma\mu h}\, F(t + h,T)\} \tag{A.5}$$

Set $s = T - t$, so that s measures the 'time to go' or the 'time left in life', and let $G(s) = F(T - s,T)$. Then

$$\frac{\partial G}{\partial s} = - (\lambda_1 + \lambda_2 + \mu)\, G(s) + \lambda_1\{f_1 + e^{-\gamma\mu h}\, G(s-h)\}$$

$$+ \lambda_2\, \{f_2 + e^{-\gamma\mu h}\, G(s-h)\} \tag{A.6}$$

The end condition on $F(t,T)$ corresponds to the initial condition $G(0) = 0$; in fact $G(s) = 0$ for all $s \le 0$. It is possible to solve Equation A.6 by the method of Laplace transforms (Bracewell, 1990). Let

$$\hat{G} = \int_0^{\infty} e^{-\omega s}\, G(s)\, ds \tag{A.7}$$

be the Laplace transform of $G(s)$. We use the following results

$$\int_0^{\infty} e^{-\omega s} ds = 1/\omega$$

$$\int_0^{\infty} e^{-\omega s}\, \frac{\partial G(s)}{\partial s} ds = \omega\hat{G}$$

$$\int_0^{\infty} e^{-\omega s}\, G(s-h)\, ds = e^{-\omega h}\, \hat{G} \tag{A.8}$$

Now multiply Equation A.6 by $e^{-\omega s}$, integrate from 0 to ∞ and use Equation A.8 to simplify

$$\omega\hat{G} = -(\lambda_1 + \lambda_2 + \mu)\ \hat{G} + [\tfrac{1}{\omega}]\ \{\lambda_1 f_1 + \lambda_2 f_2\}$$
$$+ \{\lambda_1 + \lambda_2\}\ e^{-\gamma\mu h}e^{-\omega h}\ \hat{G} \tag{A.9}$$

which can be solved for $\hat{G}$

$$\hat{G}\{\omega + \lambda_1 + \lambda_2 + \mu - \{\lambda_1 + \lambda_2\}\ e^{-\gamma\mu h}\ e^{-\omega h}\} + [\tfrac{1}{\omega}]\{\lambda_1 f_1 + \lambda_2 f_2\} \tag{A.10}$$

This equation can be written succintly by letting

$$A = \lambda_1 + \lambda_2 + \mu$$
$$B = \{\lambda_1 + \lambda_2\}\ e^{-\gamma\mu h}$$
$$C = \{\lambda_1 f_1 + \lambda_2 f_2\} \tag{A.11}$$

so that

$$\hat{G}\{\omega + A - B\ e^{-\omega h}\} = \tfrac{1}{\omega}\ C \tag{A.12}$$

or

$$\hat{G} = \frac{C}{\omega(\omega + A - B\ e^{-\omega h})} \tag{A.13}$$

Inverting this Laplace transform is easy if you know how to do it. Luckily, although I did not, my colleague Davis Cope (Department of Mathematical Sciences, North Dakota State University) did. All of the necessary formulas are found in Abramowitz and Stegun (1965); one just needs to know how to look. According to formula 29.2.6 of Abramowitz and Stegun, if $\hat{G}$ is given by Equation A.13, then

$$\frac{G(s)}{C} = \int_0^s g(s')\ ds' \tag{A.14}$$

for some function $g(t)$. In this case, the Laplace transform of $g(t)$ is given by

$$\hat{g} = \frac{1}{\omega + A - B\ e^{-h\omega}} \tag{A.15}$$

If $g(s)$ has Laplace transform Equation A.15, then $g(s)$ must have the form

$$g(s) = e^{-As}\ m(s) \tag{A.16}$$

for some function $m(s)$. This can be seen by noting that

$$\int_0^\infty e^{-\omega t}\ e^{-At}\ m(t)dt = \int_0^\infty e^{-(\omega + A)t}\ m(t)dt = \hat{m}(\omega + A) \tag{A.17}$$

where $\hat{m}(\omega)$ is the Laplace transform of $m(s)$. Combining Equations A.15 to A.17, the Laplace transform of $m(s)$ is

$$\hat{m}(\omega) = \frac{1}{\omega - Be^{Ah}\ e^{-\omega h}} \tag{A.18}$$

It is now helpful to set $D = Be^{Ah}$ and to then rewrite Equation A.18 as

$$\hat{m}(\omega) = \frac{1}{\omega} \left[\frac{1}{1 - \frac{D}{\omega} e^{-\omega h}} \right] \tag{A.19}$$

Now write the term in brackets in Equation A.19 as a power series, so that

$$\hat{m}(\omega) = \frac{1}{\omega} \left[\sum_{n=0}^{\infty} (\frac{D}{\omega})^n e^{-nh\omega} \right]$$

$$= \sum_{n=0}^{\infty} \frac{D^n}{\omega^{n+1}} e^{-nh\omega} \tag{A.20}$$

Formula 29.3.63 in Abramowitz and Stegun (1965) shows that $m(t)$ is given by

$$m(t) = \sum_{n=0}^{\infty} \frac{D^n}{n!} (t - nh)^n u(t - nh) \tag{A.21}$$

where $u(z)$ is the step function defined so that $u(z) = 1$ if $z > 0$ and $u(z) = 1/2$ if $t = 0$ and $u(z) = 0$ if $z < 0$. Thus $g(t)$ is given by

$$g(s) = e^{-As} m(s) = e^{-As} \sum_{n=0}^{\infty} \frac{D^n}{n!} (s - nh)^n u(s - nh) \tag{A.22}$$

and from Equation A.14

$$G(s) = C \int_0^s g(s') ds' = \int_0^s e^{-As'} \sum_{n=0}^{\infty} \frac{D^n}{n!} (s' - nh)^n u(s' - nh) ds' \tag{A.23}$$

Exchanging the order of integration and summation, changing the integration variables, and integrating, shows that

$$G(s) = \{\lambda_1 f_1 + \lambda_2 f_2\} \sum_{n=0}^{\infty} \frac{D^n}{n!} e^{-Anh} \gamma(n + 1, s - nh) \tag{A.24}$$

where, $D = \{\lambda_1 + \lambda_2\} e^{-\gamma \mu h} e^{Ah}$, $A = \lambda_1 + \lambda_2 + \mu$ and $\gamma(r,u)$ is the incomplete gamma function defined by

$$\gamma(r,u) = \int_0^u e^{-t} t^{r-1} dt \tag{A.25}$$

Properties of the incomplete gamma function, including methods for its computation, are given by Abramowitz and Stegun (1965, p. 260). Equation A.24 thus represents a complete solution for the lifetime fitness for times $t > t_s$ (i.e. for values of $s < T - t_s$). However, the switching time

has not been determined. Equation A.4, however, shows that the switching time can be determined by finding the time s_s satisfying the condition

$$G(s_s) = f_2 + e^{-\gamma \mu h} G(s_s - h) \qquad\qquad (A.26)$$

from which $t_s = T - s_s$. We thus have a complete solution of Equation A.4 for times greater than t_s. The solution for times less than t_s is computed in a similar fashion.