

OPTIMAL INSTAR PARASITIZATION IN A STAGE STRUCTURED HOST-PARASITOID MODEL

KATHLEEN M. CROWE
Mathematical Sciences Institute
Center for Applied Mathematics
Cornell University
Ithaca, NY 14853

J.M. CUSHING
Department of Mathematics
Interdisciplinary Program in Applied Mathematics
University of Arizona
Tucson, AZ 85721

ABSTRACT. A stage structured host-parasitoid model is derived and the equilibria studied. It is shown under what conditions the parasitoid controls an exponentially growing host in the sense that a coexistence equilibrium exists. Furthermore, for host populations whose inherent growth rate is not too large it is proved that in order to minimize the adult host equilibrium level it is necessary that the parasitoids attack only one of the larval stages. It is also proved in this case that the minimum adult host equilibrium level is attained when the parasitoids attack that larval stage which also maximizes the expected number of emerging adult parasitoid per larva at equilibrium. Numerical simulations tentatively indicate that the first conclusion remains in general valid for the model. However, numerical studies also show that it is not true in general that the optimal strategy will maximize the number of emerging adult parasitoid per larva at equilibrium.

KEY WORDS: Host-parasitoid, biological control, nonlinear difference equations, equilibrium.

1. Introduction. Biological control by releasing natural predators, competitors, pathogens, parasites or parasitoids of a pest species has become increasingly important. The successful implementation of such control programs depends crucially on an understanding of the underlying population dynamics of the species involved. Mathematical models have been used as an aid in this understanding, particularly for predation or parasitization interactions between the host (pest) and the introduced species. Simple difference equation models have been widely used, for example, to explore theoretically the various factors that can influence a pest control program based upon introducing

natural parasites and parasitoids into a pest population. See, for example, Hassell [1978], Hochberg, Hassell and May [1990] (and the many references cited therein). Factors such as host refuges (Hassel and Moran [1976]); spatial heterogeneity of the habitat (Beddington, Free and Lawton [1975]); competing parasitic species attacking a single host (Dobson [1985]); specialist and generalist enemies attacking a common prey (Hassell and May [1986]); parasitoid and hyperparasitoid interactions (May and Hassell [1981]); density dependence (Barclay [1986], May et al. [1981]); host-parasitoid-pathogen interactions (Hochberg, Hassell and May [1990]) have been considered by means of simple models.

One major simplification in the vast majority of host parasite models considered in the literature is the lack of structure within the population. (See, however, age-structured cases studied in (Barclay [1986], Godfray and Hassell [1987], Bellows and Hassell [1988], Murdoch et al. [1987]). That is to say, modeling is done at the population level, using gross statistics such as the total population sizes of the species. Significant physiological differences among the individuals such as chronological age, body size, or life cycle stages are ignored.

Class specific effects due to age, size or life cycle stage can, however, have profound effects on the dynamics of the interacting populations. In particular, since arthropod species often undergo dramatic changes in physiology, behavior and interactions with their biological and physical environments during their life cycles, it is appropriate and important to use structured population dynamics to investigate the dynamics of such species.

Barclay [1986] introduced several age-structured models for a host-parasitoid interaction in which the parasitoid oviposits in only one larval instar of the host species. He studied the effects that various modeling assumptions and model parameters have on equilibrium levels, and in particular, that of the adult host (pest). Amongst other things, Barclay concluded that the most effective or optimal control (i.e., the lowest adult host equilibrium level) occurs when the parasitoid attacks only the youngest host larva instar.

Our goal here is to investigate the robustness of Barclay's assertion and to extend his result in several ways. First of all, we will derive and utilize a (larval) stage-structured host-parasitoid model as opposed to

an age-structured model. Thus, individual larva do not necessarily spend equal time in each stage. Secondly, unlike Barclay, we will allow the parasitoid to parasitize all larval classes according to some attack preference distribution and study the effect that this lack of specialization has on the control of the adult host population.

We will draw two major conclusions from our host-parasitoid model. First, under the assumption that the inherent growth rate of the host population is not "too large," we prove that the minimal adult host equilibrium level is obtained when the parasitoid attacks only one of the larval stages. Secondly, we will give a mathematical criterion which determines which larval stage should be parasitized in order to obtain minimal adult host equilibrium level. The biological interpretation of this criterion is that the optimal larval stage to be parasitized is that stage which, when only one stage is parasitized, yields the maximal expected number of adult parasitoid emergences per parasitized larva at equilibrium. For host populations with "large" inherent growth rates, numerical simulations lead us to the tentative conjectures that the first conclusion still holds and that the optimal strategy is unchanged, although it may not any longer be the same strategy that maximizes the number of adult parasitoid emergents.

2. The model. Let the unparasitized host larvae be divided into $m \geq 2$ stages (e.g., instars), and let $x_i(t)$, $1 \leq i \leq m$, denote the densities of host larvae in these stages at time $t = 0, 1, 2, \dots$. Let $x_{m+1}(t)$ denote the density of host adults, and let $y(t)$ denote the density of adult parasitoids at time t .

In the absence of parasitization it is assumed that the dynamics of the distribution vector of host larva and adult densities

$$\mathbf{x}(t) = [x_i(t)]_{i=1}^{m+1}$$

are governed by the matrix equation

$$(1) \quad \mathbf{x}(t+1) = A\mathbf{x}(t)$$

where the projection matrix is given by the "Usher" matrix

$$(2) \quad A = \begin{bmatrix} s_1(1 - \gamma_1) & 0 & \cdots & 0 & b \\ s_1\gamma_1 & s_2(1 - \gamma_2) & \cdots & 0 & 0 \\ & s_2\gamma_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \square & \vdots & \vdots \\ 0 & 0 & \cdots & s_m(1 - \gamma_m) & 0 \\ 0 & 0 & \cdots & s_m\gamma_m & s_{m+1} \end{bmatrix}.$$

Thus, it is assumed that all newborns are in the first class and s_i is the probability that an i th stage individual survives one unit of time, γ_i is the fraction of surviving i th stage individuals that advance to the next stage in one unit of time and b is the host adult birth rate (per unit time). In this paper we will ignore density effects in the host population dynamics. Then the coefficients

$$(3) \quad s_i \in (0, 1], \quad \gamma_i \in (0, 1], \quad b > 0$$

are constants.

We have not yet specified the unit of time in the above model. We do this now by taking the unit of time to be the time from the oviposition of a parasitoid egg to the emergence of the adult parasitoid, which is assumed fixed and independent of the host larval stage parasitized. Let $y(t)$ denote the density of adult parasitoids. In order to compare different host larval attack strategies we assume that a fraction $f(y)$ of the unparasitized larvae is parasitized in one unit of time and that this fraction is distributed over the larval stages according to a distribution vector satisfying

$$(4) \quad \phi = [\phi_i]_{i=1}^m, \quad \phi_i \in [0, 1], \quad \sum_{i=1}^m \phi_i = 1.$$

This simplex of vectors will be denoted S . Thus, the fraction

$$F_i(y) = 1 - \phi_i f(y)$$

of the i th stage escapes parasitization in one unit of time and the fraction $s_i\gamma_i F_i(y)$ survives and advances to the next larval stage in one

unit of time. This means that under parasitization the host dynamics are now governed by the nonlinear matrix equation

$$(5) \quad \mathbf{x}(t+1) = A(y(t))\mathbf{x}(t)$$

$$(6) \quad A(y) = \begin{bmatrix} s_1(1-\gamma_1)F_1(y) & 0 & \cdots & 0 & b \\ s_1\gamma_1F_1(y) & s_2(1-\gamma_2)F_2(y) & \cdots & 0 & 0 \\ & s_2\gamma_2F_2(y) & \cdots & 0 & 0 \\ \vdots & \vdots & \square & \vdots & \vdots \\ 0 & 0 & \cdots & s_m(1-\gamma_m)F_m(y) & 0 \\ 0 & 0 & \cdots & s_m\gamma_mF_m(y) & s_{m+1} \end{bmatrix}$$

The adult parasitoid density satisfies the difference equation

$$(7) \quad y(t+1) = \left[\sum_{i=1}^m n_i \sigma_i \phi_i x_i(t) \right] f(y(t)) + \sigma y(t)$$

where n_i is the number of adult parasitoids that emerge from an i th stage host larva, σ_i is the survival probability of emerging adult parasitoids, and σ is the survival probability of adult parasitoids,

$$(8) \quad \sigma_i, \sigma \in [0, 1], \quad n_i = 1, 2, 3, \dots$$

The fraction $f = f(y)$ of host larvae that is parasitized per unit time is assumed to be an increasing function of adult population density. Mathematically, this means

$$(9) \quad f \in C^1([0, +\infty), [0, 1]), \quad f' > 0, \quad f(0) = 0.$$

This implies that the limit $f(+\infty) = f_\infty \leq 1$ exists and represents the maximal fraction of unparasitized larvae that can be parasitized in one unit of time by the parasitoid population. Examples include $f = f_\infty(1 - e^{-ay})$ and $f = f_\infty y/(a + y)$, $a > 0$.

If all $\gamma_i = 1$ then the projection matrix A becomes a Leslie matrix and the model in effect reduces to an age-structured model as considered by Barclay [1986]. However, unlike Barclay's model we allow stage specific survival s_i , parasitoid attacks on multiple larval stages, and multiple

(larval stage specific) adult parasitoid emergents per parasitized larva n_i .

We have assumed that the adult parasitoids cause no host mortality except to the host larvae although this and any other kinds of interactions between the host and parasitoid populations could be included in the model by assuming that the appropriate model parameters depend on the other species densities. Furthermore, density dependence can be included in the model by assuming that any of the model parameters are dependent on appropriate components of the unparasitized host density distribution vector x or on the adult parasitoid density y . For example, density dependent larval or adult host mortality or parasitoid adult mortality would involve assuming such a dependence in the parameters s_i , σ_i or σ . Similarly, the stage transition probabilities (or larval growth probabilities) γ_i , the number of oviposited parasitoid eggs per larva host n_i , the attack distribution vector ϕ and the host adult fertility rate b could be taken as density dependent. We will not consider such (presumably stabilizing) factors in this paper in order to concentrate on the host-parasitoid interaction.

3. Analysis. Our goal is to understand the equilibrium properties of the model equations (5)–(7) and to find what attack distribution ϕ minimizes the adult host density equilibrium level x_{m+1} . First we consider the host population in the absence of the parasitoid population. The assumptions (3), (4), (8) and (9) are in force throughout.

3.1. In the absence of parasitoids. The dynamics of the host population governed by the discrete matrix equation (1) are determined by the eigenvalues of the projection matrix (2). From the characteristic polynomial of this matrix given by

$$(\lambda - s_{m+1}) \prod_{i=1}^m (\lambda - s_i(1 - \gamma_i)) - b \prod_{i=1}^m s_i \gamma_i$$

it is not difficult to see that all eigenvalues lie inside the complex unit circle if $b < b_{cr}$ and there exists a real eigenvalue greater than 1 if

$b > b_{cr}$ where

$$\begin{aligned} b_{cr} &\doteq (1 - s_{m+1}) \prod_{i=1}^m \frac{1 - s_i(1 - \gamma_i)}{s_i \gamma_i} \\ &= (1 - s_{m+1}) \prod_{i=1}^m \left[1 + \frac{1 - s_i}{s_i \gamma_i} \right]. \end{aligned}$$

Thus, if $b < b_{cr}$ the population dies out exponentially and there exist constants $k > 0$ (depending only on the initial population distribution $\mathbf{x}(0) \geq 0$) and $0 < \eta < 1$ such that

$$(10) \quad 0 \leq |\mathbf{x}(t)| \leq k\eta^t, \quad t = 0, 1, 2, \dots$$

If $b > b_{cr}$ then the population grows exponentially.

Since the host population dies out exponentially if $b < b_{cr}$ it is not, in the long run, a pest. Therefore we assume throughout the rest of this paper that $b > b_{cr}$. In the next section we turn our attention to questions of whether the parasitoid population can successfully control (i.e., bring to equilibrium) this exponentially growing host population and, if so, what attack strategy will minimize the host adult population density.

3.2. The host-parasitoid model. In this section we will study the dynamics of the nonlinear host-parasitoid model equations (5)–(7). In particular, we will consider the existence of positive (coexistence) equilibria and determine, under certain conditions, which attack strategy $\phi = [\phi_i]$ will minimize the adult host equilibrium level.

We begin by recalling that if $b < b_{cr}$ then as $t \rightarrow +\infty$ the host population dies out exponentially in the absence of the parasitoid; see (10). It is only biologically reasonable that for $b < b_{cr}$ the host population should also die out in the presence of the parasitoid. Mathematically, this can be seen from the host-parasitoid equations (5)–(7) as follows. Note that for any solution starting at nonnegative initial values the host population distribution $\mathbf{x}(t)$ must satisfy the inequalities

$$0 \leq \mathbf{x}(t+1) \leq A\mathbf{x}(t)$$

(because all $F_i(y) \in [0, 1]$). It follows by a simple induction argument that such a solution $\mathbf{x}(t)$ must be dominated at each time t by the

corresponding solution of the linear matrix equation (1). Therefore, $\mathbf{x}(t)$ must also satisfy the bound (10) and consequently tend to zero as $t \rightarrow +\infty$ if $b < b_{cr}$. Of course, it is expected that the parasitoid population will also then die out. To see this mathematically, note from (7) that for all $t = 0, 1, 2, \dots$,

$$0 \leq y(t+1) \leq c\eta^t + \sigma y(t)$$

where $c \doteq k \sum_{j=1}^m n_j \sigma_j$. By induction it follows that

$$\begin{aligned} 0 \leq y(t) &\leq \sigma^{t-1}y(0) + \sum_{i=0}^{t-1} \sigma^{t-i}c\eta^i \\ &\leq \sigma^{t-1}y(0) + c \sum_{i=0}^{t-1} \mu^{t-i}\mu^i = \sigma^{t-1}y(0) + ct\mu^t \end{aligned}$$

where $\mu \doteq \max\{\sigma, \eta\}$. Since $\mu < 1$ it follows that $y(t) \rightarrow 0$ as $t \rightarrow +\infty$.

This means that the extinction equilibrium $(\mathbf{x}(t), y(t)) = (0, 0)$ is globally asymptotically stable when $b < b_{cr}$. However, when $b > b_{cr}$ this equilibrium is unstable. This can be seen from the linearization of the equations (5)–(7) at $(0, 0)$ which has a coefficient matrix of the block triangular form

$$\begin{bmatrix} A & \mathbf{c} \\ \mathbf{0} & \sigma \end{bmatrix}$$

where the $(m+1) \times (m+1)$ matrix A is given by (2). (Here \mathbf{c} is an unspecified column vector with which we need not be concerned.) The eigenvalues of this matrix are $\sigma < 1$ together with those of A which has a real eigenvalue greater than 1 when $b > b_{cr}$. We have proved the following preliminary result.

THEOREM 1. If $b < b_{cr}$ then the equilibrium $(\mathbf{x}, y) = (0, 0)$ of the host-parasitoid equations (5)–(7) is globally asymptotically stable. If $b > b_{cr}$ then $(0, 0)$ is unstable.

We now consider the possibility of positive (coexistence) equilibria for the host-parasitoid equations (5)–(7) when $b > b_{cr}$. The equilibrium

equations are

$$\begin{aligned}x_1 &= x_1(1-\gamma_1)F_1(y)x_1 + bx_{m+1} \\x_i &= s_{i-1}\gamma_{i-1}F_{i-1}(y)x_{i-1} + s_i(1-\gamma_i)F_i(y)x_i, \quad 2 \leq i \leq m \\x_{m+1} &= s_m\gamma_m F_m(y)x_m + s_{m+1}x_{m+1} \\y &= f(y) \sum_{j=1}^m n_j \sigma_j \phi_j x_j + \sigma y.\end{aligned}$$

A straightforward induction argument shows that these equations are equivalent to the equations

$$(11) \quad x_i = be_i(y)x_{m+1}, \quad 1 \leq i \leq m$$

$$(12) \quad x_{m+1} = b \frac{s_m \gamma_m F_m(y)}{1 - s_{m+1}} e_m(y) x_{m+1}$$

$$(13) \quad y = \frac{b}{1 - \sigma} f(y) x_{m+1} \sum_{i=1}^m \rho_i(y) \phi_i$$

where

$$\rho_i(y) \doteq n_i \sigma_i e_i(y)$$

$$e_i(y) \doteq \begin{cases} 1/(1 - s_1(1 - \gamma_1)F_1(y)) & \text{for } i = 1 \\ (\prod_{j=1}^{i-1} s_j \gamma_j F_j(y)) / (\prod_{j=1}^i [1 - s_j(1 - \gamma_j)F_j(y)]) & \text{for } 2 \leq i \leq m. \end{cases}$$

The number $e_i(y)$ is the expected time spent in stage i by a host larva if the adult parasitoid population were held fixed at level $y \geq 0$. The number $\rho_i(y)$ is the expected number of adult parasitoids that emerge from an individual larva host if the adult host population were held fixed at level $y \geq 0$ and larvae are parasitized only at the i th stage.

The equivalent equilibrium equations (11)–(13) can be solved for a positive (coexistence) equilibrium as follows. If x_{m+1} is to be positive, then x_{m+1} can be canceled from both sides of equation (12) to obtain the single scalar equation

$$1 = b \frac{s_m \gamma_m F_m(y)}{1 - s_{m+1}} e_m(y)$$

or

$$(14) \quad b = \frac{1 - s_{m+1}}{s_m \gamma_m F_m(y)} \frac{1}{e_m(y)}$$

for $y > 0$. If this equation has a positive solution $y > 0$, then equation (13) can be used to define

$$(15) \quad x_{m+1} = \frac{1}{b} \frac{y}{f(y)} \frac{1 - \sigma}{\sum_{i=1}^m \rho_i(y) \phi_i} > 0$$

after which x_i for $1 \leq i \leq m$ can be found from (11)

$$(16) \quad x_i = b e_i(y) x_{m+1} > 0, \quad 1 \leq i \leq m.$$

Thus, there exists a positive equilibrium of the host-parasitoid model equations (5)–(7) if and only if equation (14) has a positive solution $y > 0$.

The assumption (9) implies that the limit $f(+\infty) \leq 1$ exists and hence that the limits $F_i(+\infty)$, $e_i(+\infty)$, $\rho_i(+\infty)$ exist and are finite. Furthermore, under this assumption, the right hand side of equation (14) is easily seen to be an increasing function of $y > 0$ which ranges from a minimum at $y = 0$ of

$$\frac{1 - s_{m+1}}{s_m \gamma_m F_m(0)} \frac{1}{e_m(0)} = (1 - s_{m+1}) \prod_{i=1}^m \frac{1 - s_i(1 - \gamma_i)}{s_i \gamma_i} = b_{cr}$$

to a maximum at $y = +\infty$ of $b_\infty \leq +\infty$ given by

$$(17) \quad \begin{aligned} b_\infty &\doteq \frac{1 - s_{m+1}}{s_m \gamma_m F_m(+\infty)} \frac{1}{e_m(+\infty)} \\ &= (1 - s_{m+1}) \prod_{i=1}^m \frac{1 - s_i(1 - \gamma_i) F_i(+\infty)}{s_i \gamma_i F_i(+\infty)} \\ &= (1 - s_{m+1}) \prod_{i=1}^m \left(1 + \frac{1 - s_i F_i(+\infty)}{s_i \gamma_i F_i(+\infty)} \right) \\ &= (1 - s_{m+1}) \prod_{i=1}^m \left(1 + \frac{1 - s_i(1 - \phi_i f(+\infty))}{s_i \gamma_i (1 - \phi_i f(+\infty))} \right). \end{aligned}$$

It follows that there exists a unique positive solution $y > 0$ of equation (14) if and only if b lies between b_{cr} and b_∞ . This yields the following result.

THEOREM 2. There exists a positive (coexistence) equilibrium of the host-parasitoid equations (5)–(7) if and only if $b_\infty > b > b_{cr}$ and this equilibrium is unique when it exists.

From our analysis of equation (14) we see that $\lim_{b \rightarrow b_{cr}+} y = 0$ and hence from (16) and (15)

$$(18) \quad \lim_{b \rightarrow b_{cr}+} x_{m+1} = x_{m+1}^0 \doteq \frac{1}{b_{cr}} \frac{1}{f'(0)} \frac{1-\sigma}{\sum_{i=1}^m \rho_i \phi_i}$$

$$\lim_{b \rightarrow b_{cr}+} x_i = x_i^0 \doteq \frac{\rho_i}{n_i \sigma_i} \frac{1}{f'(0)} \frac{1-\sigma}{\sum_{i=1}^m \rho_i \phi_i} \quad \text{for } 1 \leq i \leq m$$

where we have defined $\rho_i \doteq \rho_i(0)$. We also see that

$$\lim_{b \rightarrow b_\infty-} y = +\infty, \quad \lim_{b \rightarrow b_\infty-} x_{m+1} = +\infty,$$

$$\lim_{b \rightarrow b_\infty-} x_i = +\infty \quad \text{for } 1 \leq i \leq m.$$

Note that the host model parameters determine the critical value b_{cr} but that both the host and the parasitoid model parameters determine the critical value (17) of b_∞ .

According to Theorem 2 in order for the adult host population to be controlled (brought to an equilibrium state) the parasitoid attack distribution $\phi = [\phi_i]_{i=1}^m$ and the total fraction $f(+\infty)$ of host larvae that are parasitized per unit time at large adult parasitoid population levels must be so that b_∞ given by (17) exceeds b .

Let us suppose then that $b_{cr} < b < b_\infty$. We wish next to determine what attack distribution vector ϕ will minimize the adult host equilibrium level $x_{m+1} > 0$. We will do this analytically for the case when $b \approx b_{cr}$. In this case $y \approx 0$ and $x_{m+1} \approx x_{m+1}^0$ and as a result x_{m+1} will be minimized when $b \approx b_{cr}$ if the sum

$$(19) \quad \sum_{i=1}^m \rho_i \phi_i$$

is maximized (see (18)). Since ϕ must lie on the simplex S defined by (4), it follows from a basic result in linear programming that the

maximum of the sum (19) occurs at a corner point. If we make the "generic" assumption that the ρ_i are distinct

$$(20) \quad \rho_i \neq \rho_j \quad \text{for all } i \neq j$$

then the maximum of (19) occurs at and only at a corner point of the simplex S . Since the value of the sum at the j th corner point $\phi^j = [\delta_{ij}]_{i=1}^m$

$$(21) \quad \delta_{ij} = \begin{cases} 0 & i \neq j \\ 1 & i = j \end{cases}$$

is ρ_j , it follows that the maximum occurs at the corner point ϕ^j where j is the subscript of the largest ρ_i . We have proved the following result.

THEOREM 3. Assume (20) and $b_\infty > b > b_{cr}$. For $b \approx b_{cr}$ the adult host equilibrium level will be minimized if and only if exactly one larval host stage is attacked by the parasitoid adults. Furthermore, the optimal strategy is to attack the j th stage where j is such that $\rho_j = \max\{\rho_i\}$ (where $\rho_i = \rho_i(0)$).

For b close to b_{cr} the equilibrium level of the adult parasitoids y is close to 0. Given the biological meaning of $\rho_i(y)$, this result can be interpreted as follows. If the adult host equilibrium level is to be minimized, then the parasitoids should parasitize only that larval stage of the host which results in a maximum expected total number of emerging adult parasitoids per larva at equilibrium.

We have analytically proved the optimal result given by Theorem 3 only when $b \approx b_{cr}$, that is to say, only when the host (pest) population does not grow exponentially at too great a rate in the absence of the parasitoid. We conjecture, nonetheless, that at least part of this result holds for large values of $b < b_\infty$ as well. We need to state the conjecture carefully.

As we have seen, the parasitoid can control the host (i.e., there exists a coexistence equilibrium) only if $b_\infty > b$. Since b_∞ depends on ϕ it can happen for large b that this inequality holds for some ϕ and not for other ϕ on the simplex S . Define the *feasible* set Φ to the set of $\phi \in S$ for which $b_\infty > b$. In general, for a fixed set of model parameter

values, the feasible set Φ may not be nonempty or connected or even simply connected.

For any $b > b_{cr}$ we conjecture that if the adult host equilibrium level has a minimum as a function of $\phi \in \Phi$, then this minimum must occur at a corner $\phi = \phi^j$ of the simplex S .

For b near b_{cr} the second sentence of Theorem 3 implies that the optimal parasitoid attack strategy is determined by the maximum of the quantities $\rho_i(y) \approx \rho_i \doteq \rho_i(0)$, where $y \approx 0$ is the adult parasitoid equilibrium level. Numerical simulations show that the criterion of attacking that stage corresponding to the maximum $\rho_i(y)$ is not in general true for all $b > b_{cr}$ (e.g., see Figures 2b and 3b). In other words, *it is not true in general that the optimal attack strategy that minimizes adult host equilibrium will also maximize the number of adult parasitoids emerging per larva at equilibrium.*

Our numerical simulations have shown, however, that *the optimal strategy described in Theorem 3 based on the maximum value of $\rho_i \doteq \rho_i(0)$ does remain unchanged on the feasible set.* This we tentatively take as a second conjecture about our model.

In Figure 1 adult host equilibrium levels x_3 are plotted against b and $\phi = \phi_1$ for the case of two larval stages ($m = 2$) in the model equations (5)–(7) with

$$(22) \quad f(y) = \frac{f_\infty y}{a + y}$$

and selected parameter values (see figure captions). For any value of b the minimum value of x_3 occurs when $\phi = 0$ (i.e., when only the second larval stage is attacked). Two cross sections at fixed b values are shown in Figure 2a,b, where it is clearly seen that the minimum of x_3 does occur at $\phi = 0$. It is interesting to note that x_3 is not a monotonic function of ϕ for larger values of b in Figure 1 (see also Figure 2b). This means that for these b values the worst strategy is a mixed strategy and that attacking either class alone is better than attacking both.

For the parameter values used in these graphs $\rho_2 > \rho_1$ for small b , as can be seen by the plot of the positive difference $\rho_2 - \rho_1$ in Figure 3a. This is consistent with Theorem 3. For larger b , however, $\rho_2 < \rho_1$ (as can be seen in Figure 3b) even though the minimum of x_3 still occurs at $\phi = 0$.

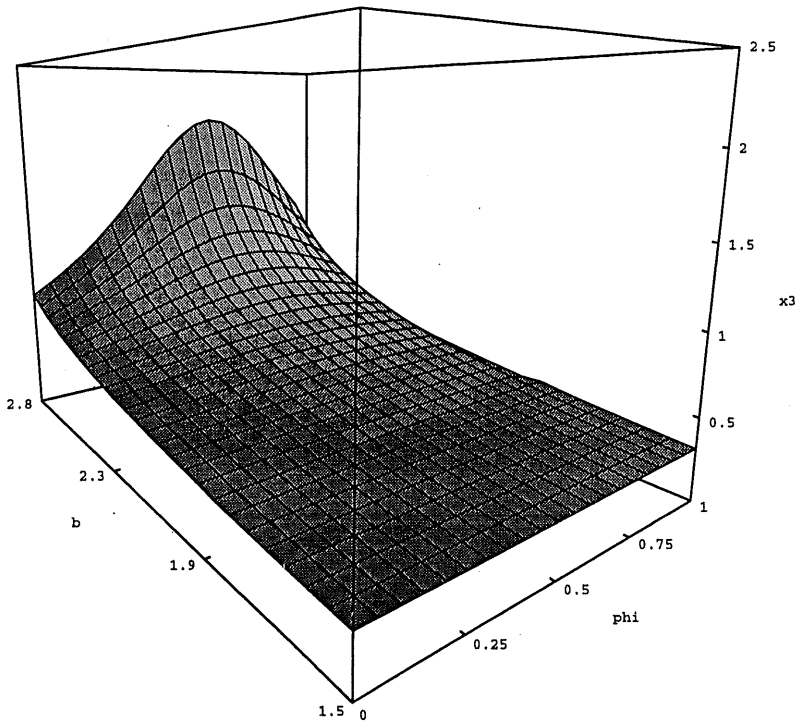


FIGURE 1. The host adult equilibrium level x_3 is plotted against b and $\phi = \phi_1$ for the case of $m = 2$ host larval stages in model equations (5)–(7) with the total fraction of larva parasitizes given by (22). Model parameter values are $s_1 = 0.4$, $s_2 = 0.6$, $s_3 = 0.8$, $\gamma_1 = 0.7$, $\gamma_2 = 0.3$, $n_1 = 13$, $n_2 = 20$, $\sigma_1 = 0.3$, $\sigma_2 = 0.5$ and $\sigma = 0$.

Theorems 2 and 3 deal only with the existence of positive coexistence equilibria. The stability properties of these equilibria are also important, of course. The positive coexistence equilibria guaranteed by Theorem 2 give rise to a continuum of host-parasitoid coexistence equilibria (x, y) that bifurcates from the equilibrium $(x^0, 0)$ as the parameter b increases through the critical value b_{cr} . Recall that the extinction state $(x, y) = (0, 0)$ is stable for $b < b_{cr}$ and unstable for $b > b_{cr}$. This kind of “supercritical” bifurcation of positive equilibria, with the loss of stability of the “trivial” equilibrium $(0, 0)$, is generally associated with a stable bifurcation, at least near the bifurcation point (see Cushing

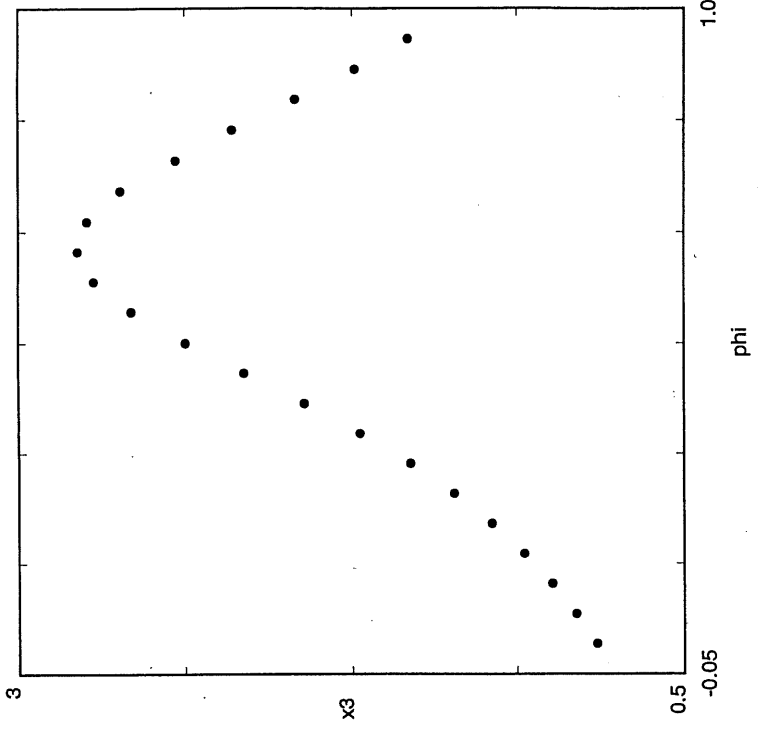
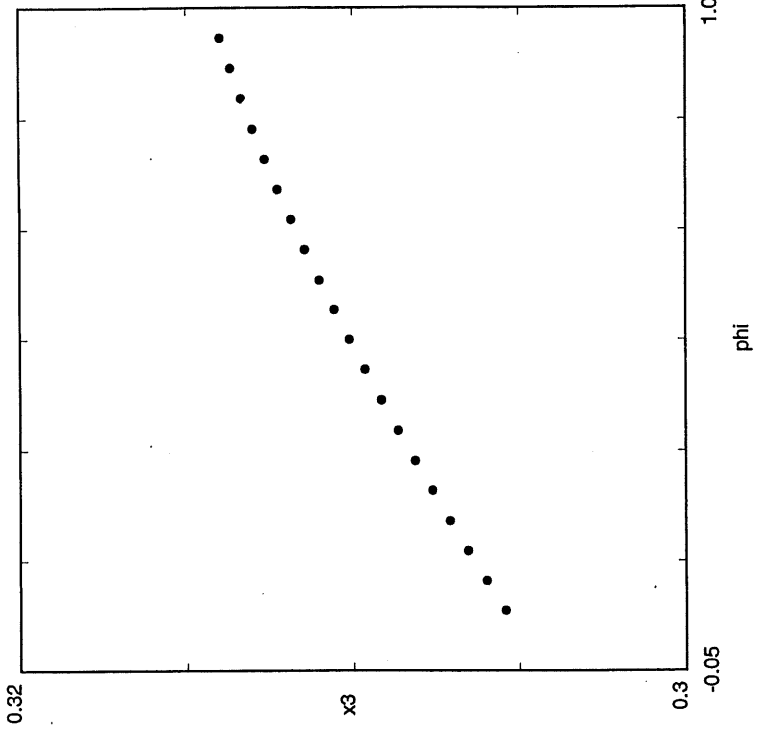


FIGURE 2. Cross sections of the 3D graph in Figure 1 are shown for (a) $b = 1.5$ (left) and (b) $b = 2.8$ (right).

[1988, 1993]). Thus, we expect that the bifurcating positive coexistence equilibria in Theorem 2 will be stable at least for b near b_{cr} . However, it turns out that the equations (1)–(2) fall into a “degenerate” case to which the general theorems that guarantee stability for supercritical bifurcations do not apply. This is because in our model the dynamics of the host population in the absence of parasitoids are governed by a linear model (1). The eigenvalue $\lambda = 1$ of linearization of the host-parasitoid equations (5)–(7) at $(x, y) = (x^0, 0)$, $b = b_{cr}$ is *not* simple as is required in the general theory. Specifically, the coefficient matrix of this linearization has the block triangular form

$$\begin{bmatrix} A & c \\ 0 & 1 \end{bmatrix}$$

where A is given by (2). Since A has 1 as a simple eigenvalue when $b = b_{cr}$, it follows that 1 is an algebraically *double* eigenvalue of this block triangular matrix.

We will not analytically study the stability of the coexistence equilibria for b near b_{cr} . In all computer simulations we made, including those used to generate Figures 1–3, global equilibrium stability was observed for all parameter values tested.

At this point we know that both populations die out if $b < b_{cr}$ and there exists a positive coexistence equilibrium if $b_{cr} < b < b_{\infty}$. In conclusion, we show that for the remaining values of $b > b_{\infty}$ both populations grow exponentially, i.e., the parasitoid fails to control the host population. To see this note that since $F_i(y)$ is a decreasing function which is bounded below by $F_i(+\infty)$ it follows that for any solution of the host-parasitoid equations (5)–(7), starting with nonnegative initial values, we have that

$$x(t+1) \geq A(+\infty)x(t) \geq 0$$

where the matrix $A(+\infty)$ is given by

$$\begin{bmatrix} s_1(1 - \gamma_1)F_1(+\infty) & 0 & \cdots & 0 & b \\ s_1\gamma_1F_1(+\infty) & s_2(1 - \gamma_2)F_2(+\infty) & \cdots & 0 & 0 \\ & s_2\gamma_2F_2(+\infty) & \cdots & 0 & 0 \\ \vdots & \vdots & \square & \vdots & \vdots \\ 0 & 0 & \cdots & s_m(1 - \gamma_m)F_m(+\infty) & 0 \\ 0 & 0 & \cdots & s_m\gamma_mF_m(+\infty) & s_{m+1} \end{bmatrix}$$

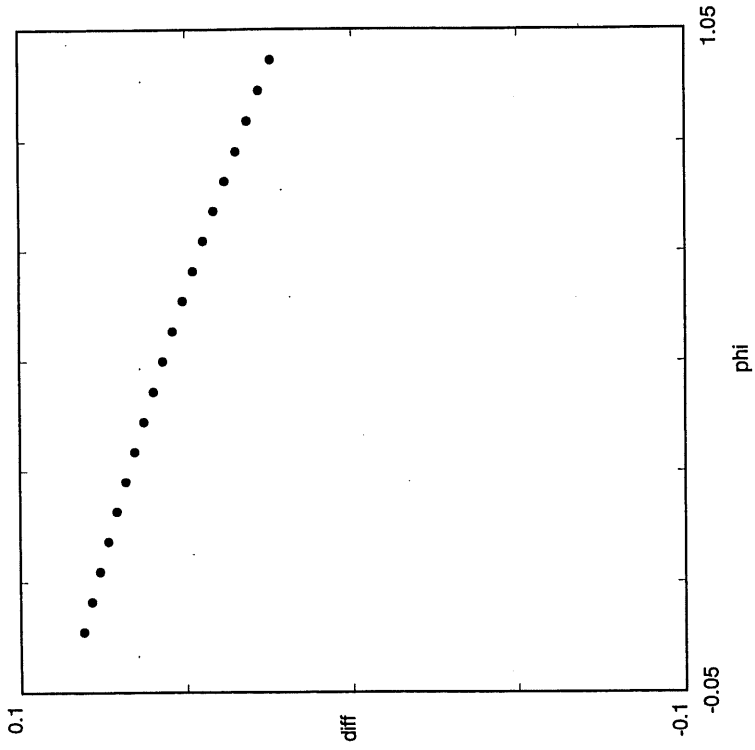
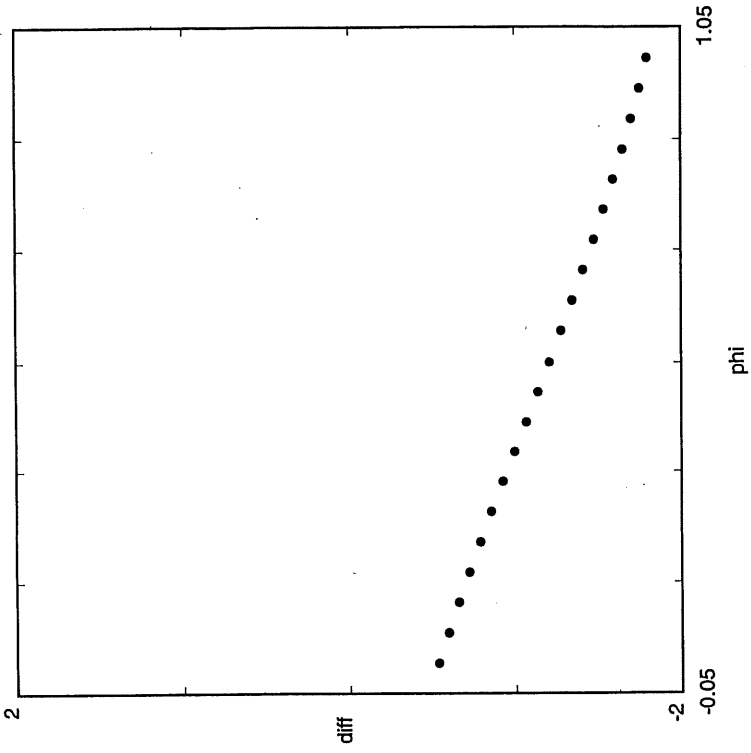


FIGURE 3. For the cross sections in Figure 2 the difference $\text{diff} = \rho_2(y) - \rho_1(y)$ is plotted against ϕ . Here y is the equilibrium value of the adult parasitoids. In (a) (left) this difference is positive while in (b) (right) it is negative.

It follows by induction that

$$\mathbf{x}(t) \geq \mathbf{z}(t) \geq 0.$$

where $\mathbf{z}(t)$ is the solution of

$$\mathbf{z}(t+1) = A(+\infty)\mathbf{z}(t), \quad \mathbf{z}(0) = \mathbf{x}(0).$$

The asymptotic behavior of $\mathbf{z}(t)$ is consequently determined by the eigenvalues of the matrix $A(+\infty)$ whose characteristic polynomial is

$$(\lambda - s_{m+1}) \prod_{i=1}^m (\lambda - s_i(1 - \gamma_i)F_i(+\infty)) - b \prod_{i=1}^m s_i \gamma_i F_i(+\infty).$$

As with the linear equation (1) and its coefficient matrix (2) it is not difficult to see that there exists a real eigenvalue greater than 1 if b exceeds the number

$$(1 - s_{m+1}) \prod_{i=1}^m \frac{1 - s_i(1 - \gamma_i)F_i(+\infty)}{s_i \gamma_i F_i(+\infty)}.$$

From (17) we see that this number is precisely b_∞ . Thus, for $b > b_\infty$ the vector $\mathbf{z}(t)$, and hence $\mathbf{x}(t)$, grows (exponentially) without bound as $t \rightarrow +\infty$. From equation (7) it easily follows that $y(t)$ also grows (exponentially) without bound.

THEOREM 4. If $b > b_\infty$, then the solutions of the host-parasitoid equations (5)–(7) are exponentially unbounded as $t \rightarrow +\infty$.

Thus, when $b > b_\infty$ the parasitoid cannot control the host population.

4. Concluding remarks. We have derived a stage structured host-parasitoid model in which parasitoid adults are allowed to attack a distribution of larval stages or instars. Using this model we showed that an exponentially growing host population ($b > b_{cr}$ in (1)) is controlled by the parasitoid if and only if the parasitoid attack distribution vector ϕ and the maximal fraction of host larvae that can be parasitized in one unit of time $f_\infty = f(+\infty)$ are such that $b_\infty > b$. In this case

there exists a host-parasitoid coexistence equilibrium. For hosts whose inherent exponential growth rate is not too large (i.e., for b near the critical value b_{cr}) we used our model to prove that the optimal control of the adult host, in the sense that minimal adult host equilibrium level is obtained, requires that only one of the larval host stages be parasitized. We conjecture that this conclusion remains valid for all b .

For b near the critical value b_{cr} we also proved that the optimal larval stage to attack is that stage which results in the maximal expected number of emerging adult parasitoids (per larva) at equilibrium (i.e., the stage with maximum $\rho_i(0)$). Numerical simulations show that this same strategy, which is determined when b is near b_{cr} and adult parasitoid equilibrium levels are low (technically 0), remains the optimal strategy for *all* feasible $b > b_{cr}$ and this we tentatively conjecture as generally true for our model populations. However, in general it is not true for all b that the optimal strategy that minimizes host adult equilibrium levels is the same strategy that maximizes the number of emerging adult parasitoids (per larva) at equilibrium (i.e., that maximizes $\rho_i(y)$). The graphs in Figures 2b and 3b illustrate this fact.

Our results corroborate and extend one of Barclay's main conclusions in (Barclay [1986]). From his age-structured model ($\gamma_i = 1$) Barclay concludes that the optimal strategy is for the parasitoids to attack the youngest larvae. In Barclay's model the larval stages all produce an equal number of surviving emerging adult parasitoids (all $n_i = 1$ and all σ_i are equal) and the parasitoids attack only one larval age class. Clearly under these conditions ρ_1 is the largest of the ρ_i .

Mathematically, we have only investigated the existence of positive coexistence equilibrium solutions to our model host-parasitoid equations. We have given no proof of stability, although based upon common bifurcation principles we conjecture equilibrium stability at least for b near b_{cr} . Numerical simulations show global stability for all parameter values tested. We hope in future work to investigate these stability issues, including the possibility of nonequilibrium dynamics (cycles and "chaos"), as well as the case of density dependent models.

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