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Optimal parasitization in a size-structured host-parasitoid model

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Abstract. A continuous size-structured model for a host-parasitoid interaction is derived and analyzed. Parasites attack only immature hosts according to a size-specific preference (probability) distribution ψ. We investigate the problem of how to determine ψ so as to minimize the equilibrium level of the adult host (pest) population. It is shown that this problem is equivalent to that of maximizing the expected number of parasitoid emergences (per immature host) of an adult parasitoid over the course of its life time. Under certain further conditions it is shown that this maximization is obtain by (and only by) parasitization that is concentrated on certain specified immature size classes.

1. Introduction

The success of a biological control program based upon the release of predators, pathogens, competitors or parasites into a pest population depends crucially on an understanding of the dynamics of the populations involved. Simple mathematical models have been used to help in this understanding, particularly with regard to predation and parasitization of the pest species by the introduced species (see for example [1], [2], [5], [6], [7], [8], [3], [9], [10], [12], [15], [17], [16]). It is often the case that parasites attack specific life cycle stages of their hosts. Arthropod species form a notable example since they often undergo dramatic changes in physiology and behavior during their life cycles. However, most models appearing in the literature do not account for the dynamics of life cycle stages, modeling instead the dynamics of some gross population statistic such as total population size or biomass. Some exceptions, in the case of host-parasite interactions, include [1], [5], [7], [3], [17]. A deeper understanding of the dynamics of such host-parasitoid

interactions requires models that take into account significant physiological and/or behavioral differences among the individuals in different life cycles stages.

Barclay [1] studies several nonlinear discrete (Leslie-type) age-structured models for arthropod host-parasitoid interactions in which the parasitoid attacks and oviposits in only one larval instar of the host. It is assumed that each instar lasts the same time duration and therefore is determined by the chronological age of the larva. Under his model assumptions, Barclay concludes that optimal pest control (defined as minimum adult host equilibrium level) is attained by parasitizing the youngest host larval instar. In [5] the robustness of Barclay's conclusions was investigated in a couple of directions. More general stage-structured discrete models were derived in which the time durations of instars are not necessarily the same and in which parasitization was distributed over all instars, not necessarily focussed on a single instar stage. It was then proved that in order to attain optimal control it is necessary to parasitize a single instar stage and the stage to be parasitized was characterized (in terms of maximal adult parasitoid emergents per larva).

Our goal in this paper is to further investigate the robustness of these conclusions concerning the optimal strategy for a host-parasitoid control program. Specifically, we will derive a continuous host-parasitoid model in which parasites attack host immatures according to some preference (or probability) distribution and consider the question of what parasitization distribution will reduce the adult host (pest) to its lowest equilibrium level. The model will allow for varied growth and survivorships during the immature stages. It is derived in Sec. 2. In Sec. 3 the integro-partial differential equations are analyzed. We will not concern ourselves with the technical problems associated with existence and uniqueness of solutions, but instead concentrate on the existence of equilibrium solutions and their properties. In this paper (as in [5]) the host population model in the absence of parasitization is linear and therefore exhibits exponential growth. This is a mathematically simplifying assumption and is relevant to the case when the host (pest) population is in an exponential growing phase. The model investigates the problem of controlling an exponentially growing pest, as opposed to a pest near equilibrium. (We hope to consider the latter problem, which introduces further nonlinear interactions, in future research.) The conditions necessary to "control" the host by ceasing its exponential growth and minimizing the resulting equilibrium level of its adult population are derived and interpreted. While we do not solve the minimization problem in general, we show that its approximate solution (at low parasitoid equilibrium densities relative to that of the host) is, roughly speaking, attained by concentrating the parasitization distribution on a single size class of immatures, namely that which maximizes the expected number of parasitoid emergences per larva per adult parasite. The technical mathematical details appear in the Appendix.

2. The model

For the host population in the absence of parasitization we adopt a McKendrick–von Foerster type continuous linear size-structured model

$$
\begin{aligned}
\partial_t x + \partial_s(gx) &= -\mu(s)x \\
g(s_b)x(t, s_b) &= \int_{s_m}^{+\infty} \beta x(t, s)\,ds \\
x(0, s) &= x_0(s).
\end{aligned}
\tag{1}
$$

$x(t, s)$ is the per unit size density of *unparasitized* hosts of size s at time t. The coefficient $g(s) = ds/dt$ is the growth rate of an individual unparasitized host of size s and β is the unparasitized host per capita birth rate. The only removals from the population in the absence of parasitization is by death and $\mu(s)$ is the size-specific per capita death rate. The quantities s_b and s_m ($0 \leq s_b < s_m < +\infty$) denote the unparasitized host size at birth and the size at onset of reproduction, respectively. $x_0(s)$ is the initial size distribution.

In order to specify the model we must have submodels for the vital rates g, μ, and β. In the absence of parasitization we will assume that the unparasitized host population grows exponentially. Thus, mathematically we ignore density effects on the vital rates g, β, and μ. For simplicity we assume that $\beta > 0$ is constant. Since, as explained in the introduction, we wish to allow for size specific vital rates, both $g = g(s)$ and $\mu = \mu(s)$ will be assumed size dependent. In our analysis below we will require that these two vital rates have a certain amount of smoothness. Sufficient for this are the assumptions that $\mu(s) \geq 0$ is continuously differentiable and $g(s)$ is twice continuously differentiable for $s > s_b$ and that $g(s)$ is bounded away from zero and $+\infty$: $0 < g_m \leq g(s) \leq g_M < +\infty$. Note that there is a one-to-one relationship between an individual's size s and the time t taken to grow to that size which is given by the formula $t = \int_{s_b}^{s} (1/g(\sigma))\,d\sigma$.

In the presence of parasitization the removal rate, as modeled by the right hand side of the partial differential equation (1), must be modified in order to account for those individuals removed by parasitization. Let $\psi(s)$ be a probability distribution function, with $\operatorname{supp} \psi \subseteq [s_b, s_m]$, such that $\psi(s)\Delta s$ gives the probability that an immature host is parasitized (per adult parasitoid) while in the size class s to $s + \Delta s$. If $f(y)$ is the number of potential adult parasitoid encounters when the adult parasitoid population is at level y, then the probability that a host immature survives parasitization while in the size class s to $s + \Delta s$ is given by $(1 - \psi(s)\Delta s)^{f(y)}$. Here each encounter is treated as an independent event. If the size interval from s_b to s is divided into n subintervals of size Δs and survival from parasitization over each subinterval is assumed to be an independent event, then the probability that a host immature survives parasitization until size s is given by

$$
\lim_{\Delta s \to 0} \prod_{j=1}^{n} \left(1 - \psi(s_j)\Delta s\right)^{f(y_j)} = \exp\left(-\int_{s_b}^{s} \psi(\sigma) f(y(t(\sigma)))\,d\sigma\right)
$$

where $t(s) = t_0 + \int_{s_b}^{s} (1/g(\sigma)) d\sigma$.

The probability that an immature host is parasitized (per adult parasitoid) during a time interval t to $t + \Delta t$ (during which time it is in the size class s to $s + \Delta s$) is given by $\psi(s)\Delta s = \psi(s)\frac{\Delta s}{\Delta t}\Delta t = \psi(s)g(s)\Delta t$. Thus, the per host rate of removal (per unit time) due to parasitization is given by $\psi(s)g(s)f(y)$ and the right hand side of the partial differential equation in (1) must be modified by the addition of the term $-\psi(s)g(s)f(y)x$. We then obtain the equations

$$\begin{aligned}
\partial_t x + \partial_s(gx) &= -\left(\mu(s) + \psi(s)g(s)f(y)\right)x \\
g(s_b)x(t, s_b) &= \int_{s_m}^{+\infty} \beta x(t, s)ds \\
x(0, s) &= x_0(s)
\end{aligned} \tag{2}$$

for the unparasitized host population in the presence of parasitoids. Note that we only model the unparasitized hosts; although parasitization may not be lethal to an individual we assume parasitized hosts cannot reproduce. Here $\psi(s)$ is a probability density function

$$\psi : [s_b, +\infty] \to [0, +\infty), \text{ supp } \psi \subseteq [s_b, s_m], \quad \int_{s_b}^{s_m} \psi(s)ds = 1.$$

We will refer to ψ as the "parasitization preference distribution". With regard to the number of per host parasitoid encounters $f(y)$, as a function of adult parasitoid numbers y, we assume

$$f \in C^1[0, +\infty), \quad f' > 0, \quad f(0) = 0, \quad \text{and} \quad \lim_{y \to +\infty} f(y) = f_\infty < +\infty.$$

Finally, we need a dynamical equation for the total adult parasitoid population $y = y(t)$. Let $t_i \geq 0$ be the incubation time for parasitoids and let

$$\pi = \pi(t_i) \in [0, 1]$$

denote the probability that a parasitoid egg produces an emergent parasitoid in t_i units of time. For example, one assumption might be that the death rate of a parasitized host is δ_h and that pre-emergent parasitoid mortality is the same as that of its host, in which case $\pi = \exp(-\delta_h t_i)$. Let $n(s)$ denote the number of parasitoid eggs that are oviposited in a immature host of size s. Finally, let $\delta \geq 0$ be the per capita adult parasitoid death rate (assumed to be constant). Under these assumptions we have the delay differential equation

$$y'(t) = \pi(t_i)f(y(t - t_i)) \int_{s_b}^{s_m} n(s)\psi(s)g(s)x(t - t_i, s)ds - \delta y(t) \tag{3}$$

for the adult parasitoid population y.

The coupled system (2)–(3) constitutes our host-parasitoid model.

3. Analysis

In this section we analyze equilibrium solutions of the model equations (2)–(3) and determine some of their stability properties. We also study the problem of minimizing the adult host equilibrium population and determine, for sufficiently low levels of parasitoid equilibrium levels, the approximate optimal parasitization preference distribution $\psi(s)$ that accomplishes this minimization. We begin with the host population in the absence of parasitization.

3.1. Host dynamics in the absence of parasitoids

In the absence of parasitoids, the host dynamics satisfy the linear model (1). An integration of the equations

$$\frac{dt}{d\eta} = 1$$

$$\frac{ds}{d\eta} = g(s)$$

$$\frac{dx}{d\eta} = -(\mu + \frac{dg}{ds})x$$

for the characteristics yields

$$x(t, s) = \begin{cases} x(t - \tau, s_b) \, e^{-\int_{s_b}^{s} \mu(z)/g(z)dz} \frac{g(s_b)}{g(s)}, & t \geq \tau(s) \\ x_0(s(\tau - t)) \, e^{-\int_{s(\tau-t)}^{s} \mu(z)/g(z)dz} \frac{g(s(\tau-t))}{g(s)}, & t < \tau(s) \end{cases} \qquad (4)$$

where $\tau = \tau(s) = \int_{s_b}^{s} dx/g(x)$ is the time required for an individual to grow from size s_b to size s, and where $s(\tau - t)$ is the size of an individual of age $\tau - t$. Substitution of (4) into the birth equation in (1) gives

$$x(t, s_b) = \int_{s_m}^{+\infty} \beta x \left(t - \int_{s_b}^{s} dz/g(z), s_b \right) e^{-\int_{s_b}^{s} \mu(z)/g(z)dz} \frac{1}{g(s)} ds \qquad (5)$$

for large t.

Setting $x(t, s) = q(s)e^{\lambda t}$ we derive from (5) the characteristic equation

$$1 = \int_{s_m}^{+\infty} \beta e^{-\lambda \int_{s_b}^{s} dz/g(z)} e^{-\int_{s_b}^{s} \mu(z)/g(z)dz} \frac{1}{g(s)} ds \qquad (6)$$

for λ. Define

$$\beta_{cr} \doteq \frac{1}{\int_{s_m}^{+\infty} \exp\left(-\int_{s_b}^{s} \mu(z)/g(z)dz\right) \frac{1}{g(s)}ds}.$$

If $\beta > \beta_{cr}$ then the right hand side of equation (6) equals $\beta/\beta_{cr} > 1$ when $\lambda = 0$ and decreases monotonically to 0 as $\lambda \to +\infty$. Thus, equation (6) has a positive real root, which implies that $x(t, s)$ grows exponentially as $t \to +\infty$ [13]. Suppose, on the other hand, that $0 < \beta < \beta_{cr}$. If λ is a root with $\text{Re}\,\lambda \geq 0$, then the right hand side is smaller in magnitude than β/β_{cr} and hence is strictly less than 1. This means that equation (6) has no roots satisfying $\text{Re}\,\lambda \geq 0$ and hence $x(t, s)$ decays to 0 as $t \to +\infty$ [13].

3.2. Analysis of the host-parasitoid model

In the following two sub-sections we study the existence of positive (coexistence) equilibria for the host-parasitoid model and minimization problem for the host adult (pest) equilibrium.

3.2.1. Equilibria analysis

Theorem 1. (a) *If $\beta < \beta_{cr}$, then the trivial equilibrium $(x, y) = (0, 0)$ of the host-parasitoid model (2)–(3) is globally attracting.*
  (b) *If $\beta > \beta_{cr}$, then $(0, 0)$ is unstable.*

Proof. (a) Let $\beta < \beta_{cr}$. The solution $x_u(t, s) \geq 0$ of the model equations (1) for the host population in the absence of parasitization decays exponentially to zero. In order to show that the trivial equilibrium is attracting, we will show that the solution $x(t, s)$ of the model equations (2) for the host population in the presence of parasitization satisfies the inequality

$$0 \leq x(t, s) \leq x_u(t, s)$$

for all sufficiently large t and for all $s \geq s_b$.
  For a given solution of (2)–(3) the host-parasitoid model (2) has characteristic equations

$$\frac{dt}{d\eta} = 1$$

$$\frac{ds}{d\eta} = g(s)$$

$$\frac{dx}{d\eta} = -(\mu + \frac{dg}{ds} + \psi g f(y))x$$

and so we have the differential inequality

$$\frac{dx}{d\eta} \leq -(\mu + \frac{dg}{ds})x,$$

which yields

$$x(t,s) \leq \begin{cases} x(t-\tau, s_b) \, e^{-\int_{s_b}^{s} \mu(z)/g(z)dz} \frac{g(s_b)}{g(s)}, & t \geq \tau(s) \\ x_0(s(\tau - t)) \, e^{-\int_{s(\tau-t)}^{s} \mu(z)/g(z)dz} \frac{g(s(\tau-t))}{g(s)}, & t < \tau(s) \end{cases}$$

where $\tau = \int_{s_b}^{s} dx/g(x)$. If we can show

$$x(t, s_b) \leq x_u(t, s_b) \text{ for all } t \geq 0,$$

then the desired result will follow from (4).

Let $x_u(t, s, \varepsilon)$ be the solution to (1) with the perturbed initial condition

$$x_u(0, s, \varepsilon) = x_0(s) + \varepsilon h(s),$$

where $h : (s_b, +\infty) \rightarrow (0, +\infty)$ is such that $h(s(\cdot)) \in L^1(0, +\infty)$ where $s = s(\eta)$ is defined by $\eta = \int_{s_b}^{s}(1/g(z))dz$. Then $x(0, s_b) < x_u(0, s_b, \varepsilon)$. First we will use Theorem 4 (induction on closed, bounded-below subsets of R) appearing in the Appendix to show

$$x(t, s_b) < x_u(t, s_b, \varepsilon) \quad \text{for all } t, \varepsilon > 0. \tag{7}$$

Then we will show that $x_u(t, s_b, \varepsilon) \rightarrow x_u(t, s_b)$ as $\varepsilon \rightarrow 0$. From these facts we will conclude that $0 \leq x(t, s_b) \leq x_u(t, s_b)$ for all $t \geq 0$.

Let $\varepsilon > 0$. For $t < 0$, define $x_u(t, s_b, \varepsilon) \doteq x_u(0, s_b, \varepsilon)$ and $x(t, s_b) \doteq x(0, s_b)$. The truth set $\{t \in R \mid x(t, s_b) < x_u(t, s_b, \varepsilon)\}$ is open in R since $x(t, s_b)$ and $x_u(t, s_b, \varepsilon)$ are continuous in t. Let $T \in [0, +\infty)$. If $T = 0$, then $x(T, s_b) < x_u(T, s_b, \varepsilon)$. If $T \neq 0$, assume $x(t, s_b) < x_u(t, s_b, \varepsilon)$ for all $t \in [0, T)$. Under this last assumption $x(T, s_b) < x_u(T, s_b, \varepsilon)$, as is verified by the following

inequalities.

$$
\begin{aligned}
g(s_b)x(T, s_b) &= \int_{s_m}^{+\infty} \beta x(T, s)ds \\
&\leq \int_{s_m}^{s(T)} \beta x(T - \tau, s_b) \, e^{-\int_{s_b}^{s} \mu(z)/g(z)dz} \frac{g(s_b)}{g(s)} ds \\
&\quad + \int_{s(T)}^{+\infty} \beta x_0\left(s(\tau - T)\right) \, e^{-\int_{s(\tau-T)}^{s} \mu(z)/g(z)dz} \frac{g(s(\tau-T))}{g(s)} ds \\
&< \int_{s_m}^{s(T)} \beta x_u(T - \tau, s_b, \varepsilon) \, e^{-\int_{s_b}^{s} \mu(z)/g(z)dz} \frac{g(s_b)}{g(s)} ds \\
&\quad + \int_{s(T)}^{+\infty} \beta \left[x_0(s(\tau - T)) \right. \\
&\qquad \left. + \varepsilon \, h(s(\tau - T)) \right] \, e^{-\int_{s(\tau-T)}^{s} \mu(z)/g(z)dz} \frac{g(s(\tau-T))}{g(s)} ds \\
&= \int_{s_m}^{+\infty} \beta x_u(T, s, \varepsilon)ds \\
&= g(s_b)x_u(T, s_b, \varepsilon)
\end{aligned}
$$

where $s(T)$ is the size at time T of an individual born at time 0. By Theorem 4 of the Appendix we conclude $x(t, s_b) < x_u(t, s_b, \varepsilon)$ for all $t \geq 0$.

It remains to show that $x_u(t, s_b, \varepsilon) \to x(t, s_b)$ as $\varepsilon \to 0$. By (4)

$$
\begin{aligned}
g(s_b) \mid x_u(t, s_b, \varepsilon) - x_u(t, s_b) \mid &= \mid \int_{s_m}^{+\infty} \beta[x_u(t, s, \varepsilon) - x_u(t, s)]ds \mid \\
&\leq \int_{s(t)}^{+\infty} \beta \varepsilon h(s(\tau - t)) \frac{g(s(\tau-t))}{g(s)} ds \\
&\quad + \int_{s_m}^{s(t)} \beta \mid x_u(t - \tau, s_b, \varepsilon) \\
&\qquad - x_u(t - \tau, s_b) \mid \frac{g(s_b)}{g(s)} ds \\
&\leq \int_0^{+\infty} \beta \varepsilon h(s(\eta)) g(s(\eta)) d\eta \\
&\quad + \int_0^t \beta \mid x_u(\eta, s_b, \varepsilon) - x_u(\eta, s_b) \mid g(s_b)d\eta.
\end{aligned}
$$

Thus, by Gronwall's Inequality

$$
g(s_b) \mid x_u(t, s_b, \varepsilon) - x_u(t, s_b) \mid \leq \beta \varepsilon g_M \int_0^{+\infty} h(s(\eta))d\eta e^{\beta t}.
$$

It follows that $x_u(t, s_b, \varepsilon) \to x_u(t, s_b)$ as $\varepsilon \to 0$ for each $t \geq 0$.

We conclude that $0 \leq x(t, s_b) \leq x_u(t, s_b)$ for all $t \geq 0$ and consequently that $x(t, s)$ tends to 0 exponentially as $t \to +\infty$.

From (3) we see that y satisfies an equation of the form $y' = \xi(t) - \delta y$ where $\xi(t) \to 0$ as $t \to +\infty$. Therefore, $y(t) \to 0$ as $t \to +\infty$, and thus $(x, y) = (0, 0)$ is globally attracting.

(b) Let $\beta > \beta_{cr}$. If we set $x(t, s) = q(s)e^{\lambda t}$, and $y(t) = ce^{\lambda t}$ in the linearization of the host-parasitoid model equations (2)–(3) at the equilibrium $(0, 0)$ we obtain as eigenvalues $\lambda = -\delta < 0$ and those values of λ for which the equation

$$
gq' + \left(\lambda + \frac{dg}{ds} + \mu(s) \right) q = 0
$$

has a nonzero solution $q \neq 0$. Substituting the general solution of this linear equation into the birth equation in (2) we again obtain the characteristic equa-

tion (6). As we have already seen $\beta > \beta_{cr}$ implies this equation has a positive root. Therefore $(0,0)$ is unstable.   □

Define the number

$$\beta_\infty \doteq \beta_{cr} e^{f_\infty} > \beta_{cr}.$$

Theorem 2. *There exists a positive (coexistence) equilibrium of the host-parasitoid model (2)–(3) if and only if $\beta_{cr} < \beta < \beta_\infty$, and this positive equilibrium is unique when it exists.*

Proof. To find a positive equilibrium (x_e, y_e), we investigate the static system derived from equations (2)–(3)

$$
\begin{array}{ll}
\text{(a)} & \frac{dx_e}{ds} = -\frac{1}{g(s)}\left(\mu(s) + \psi(s)g(s)f(y_e)\right)x_e - \frac{1}{g(s)}\frac{dg}{ds}x_e \\
\text{(b)} & y_e = \pi(t_i)\frac{1}{\delta}f(y_e)\int_{s_b}^{s_m} n(s)\psi(s)g(s)x_e(s)ds
\end{array}
\tag{8}
$$

with initial condition

$$x_e(s_b) = \frac{1}{g(s_b)}\int_{s_m}^{+\infty}\beta x_e(s)ds. \tag{9}$$

An integration of (8a) gives

$$x_e(s) = x_e(s_b)e^{-\int_{s_b}^{s}\mu(z)/g(z)dz}\frac{g(s_b)}{g(s)}e^{-f(y_e)\int_{s_b}^{s}\psi(z)dz}. \tag{10}$$

Substituting the initial condition (9) into (10) and integrating the result from s_m to $+\infty$, we find

$$\int_{s_m}^{+\infty}x_e(s)ds = \int_{s_m}^{+\infty}\beta x_e(s)ds\int_{s_m}^{+\infty}\frac{1}{g(s)}e^{-\int_{s_b}^{s}\mu(z)/g(z)dz}e^{-f(y_e)\int_{s_b}^{s}\psi(z)dz}ds,$$

or, since supp $\psi \subseteq [s_b, s_m]$,

$$\beta = \beta_{cr}e^{f(y_e)}. \tag{11}$$

Thus, there exists a unique positive equilibrium

$$0 < y_e = f^{-1}\left(\ln\left(\beta/\beta_{cr}\right)\right)$$

if and only if

$$\beta_{cr} < \beta < \beta_\infty.$$

Having found the adult parasitoid equilibrium y_e, we can in turn find a unique equilibrium distribution $x_e(s)$ for the host. Substituting (9) into (10) and the

result into (8b) we obtain an equation that can be solved for the total adult host population

$$\int_{s_m}^{+\infty} x_e(s)\,ds = \frac{\delta y_e}{\pi(t_i)\beta f(y_e) \int_{s_b}^{s_m} \left(n(s)\psi(s)e^{-\int_{s_b}^{s}(\mu(z)/g(z)+f(y_e)\psi(z))dz} \right) ds}.$$

(12)

This formula can be used in (9) and (10) to obtain the equilibrium distribution

$$x_e(s) = \frac{\delta y_e e^{-\int_{s_b}^{s}(\mu(z)/g(z)+f(y_e)\psi(z))dz}/g(s)}{\pi(t_i)f(y_e) \int_{s_b}^{s_m} \left(n(s)\psi(s)e^{-\int_{s_b}^{s}(\mu(z)/g(z)+f(y_e)\psi(z)))dz} \right) ds}. \qquad \square$$

The result in Theorem 2 can be viewed as a bifurcation phenomena as the parameter β is increased through the critical value β_{cr} at which the zero (extinction) equilibrium loses stability. Such a transcritical bifurcation is generally associated with an exchange of stability, which would led us to conjecture that the positive equilibria in Theorem 2 is locally asymptotically stable at least for β close to β_{cr}. However, because the host population in our model grows linearly in the absence of the parasites, this bifurcation is not "generic" and the formal bifurcation theorems do not apply.

We numerically investigated the stability of the positive (coexistence) equilibrium for an age-structured case which

$$g = 1, \quad s_b = 0, \quad s_m > 0, t_i = 0, \quad \pi \in [0,1]$$

$$n > 0, \quad \mu > 0, \quad \delta > 0$$

$$f(y) = \frac{by}{a+y}$$

(13)

$$\psi(s) = \begin{cases} 1/s_m & if \quad s \le s_m \\ 0 & if \quad s > s_m \end{cases}.$$

For this example Theorems 1 and 2 imply that the zero equilibrium loses stability at $\beta_{cr} = \mu e^{\mu s_m}$ and there exists a unique positive equilibrium for each β in the interval $(\beta_{cr}, \beta_\infty) = [\mu e^{\mu s_m}, \mu e^{b+\mu s_m}$. Figure 1 illustrates these facts by means of a numerically computed bifurcation diagram. Our numerical results indicate that the positive equilibria are global attracting. See Figure 2.

Caption for Figure 1: Positive equilibrium values of the unparasitized juvenile population $J = \int_0^{s_m} x(t,s)ds$, the unparasitized adult host population $A = \int_{s_m}^{\infty} x(t,s)ds$ and the adult parasitoid population y for the eqations (2)–(3) with (13) and $s_m = 1, \pi = 0.1, n = \mu = \delta = b = a = 1$ are plotted against the parameter $\beta \in (\beta_{cr}, \beta_\infty) = (e, e^2)$. Note the vertical asymptote at $\beta_\infty = e^2$.

Caption for Figure 2: Graphs of J, A and y against time t are shown for serveral different initial conditions in the example described in Figure 1 with $\beta = 3.5$.
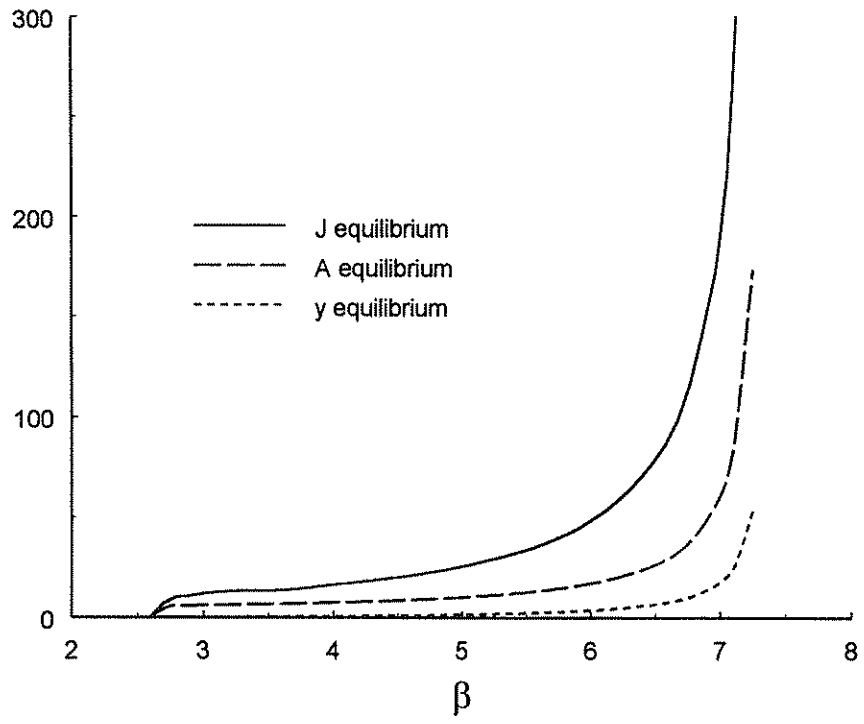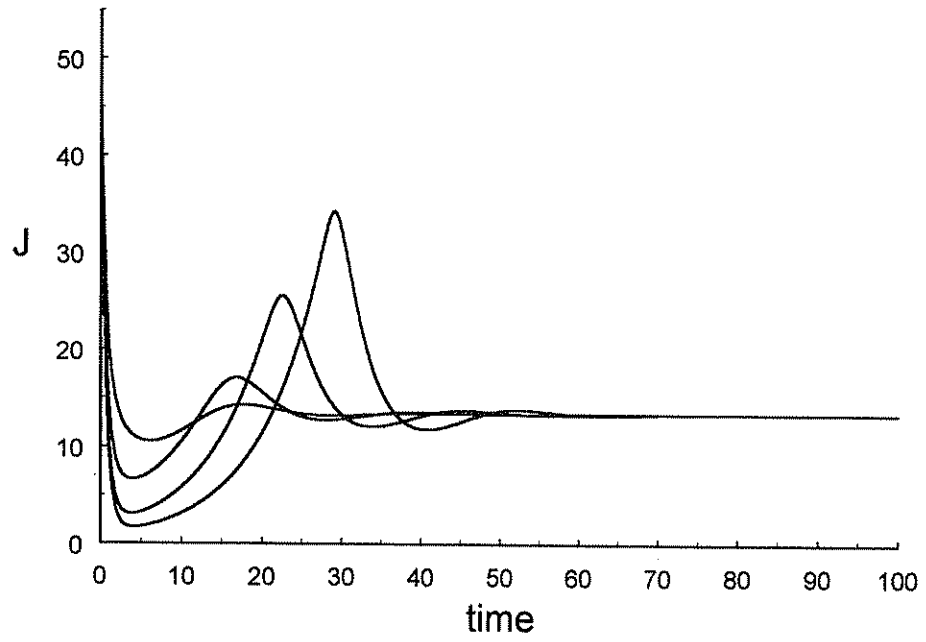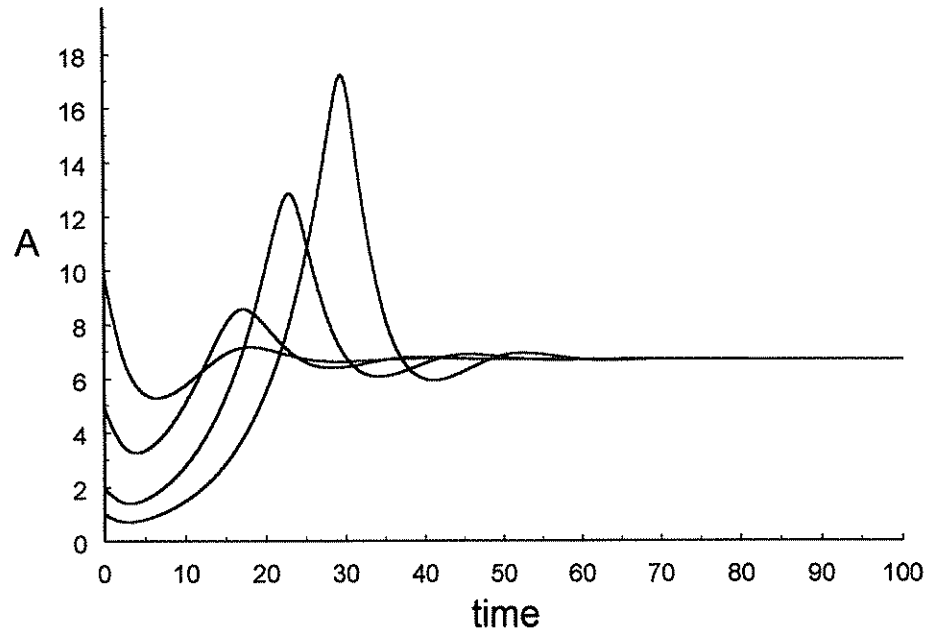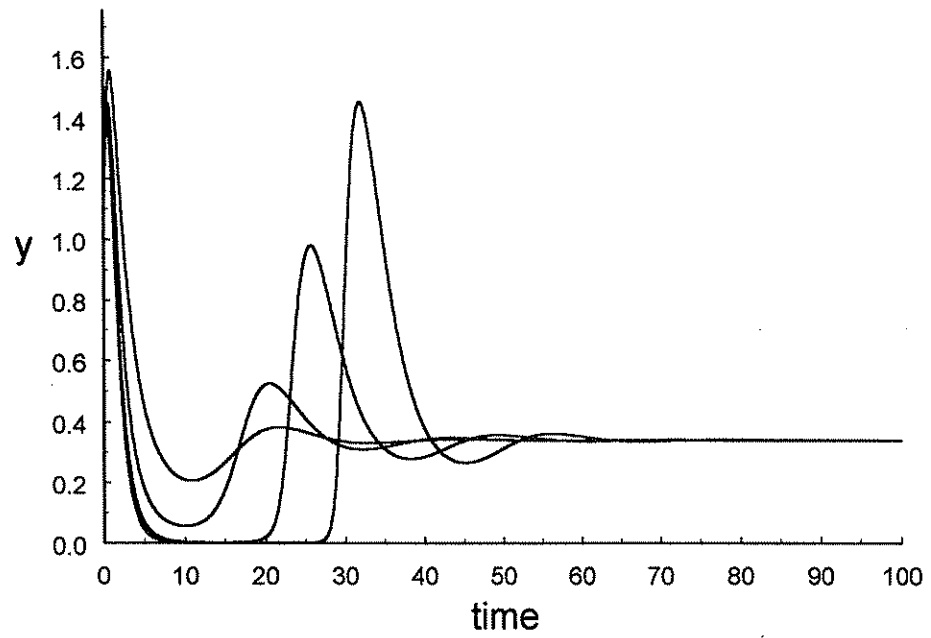
Figure 1

Figure 2a

Figure 2b

Figure 2c

3.2.2. Minimization of the adult host population

Our goal is to minimize the equilibrium adult host population, as given by the complicated expression on the right hand side of the formula (12), by an appropriate choice of the immature parasitization distribution function $\psi(s)$.

First we note that the formula (12) for the equilibrium adult host population can be written

$$\beta \int_{s_m}^{+\infty} x_e(s)\,ds\, E(\psi) = 1 \tag{14}$$

where

$$E(\psi) \doteq \frac{1}{\delta} \int_{s_b}^{s_m} \left(\pi(t_i) n(s) \frac{f(y_e)\psi(s)g(s)}{y_e} e^{-\int_{s_b}^{s}(\mu(z)/g(z)+f(y_e)\psi(z))\,dz} \right) \frac{1}{g(s)}\,ds. \tag{15}$$

The exponential appearing in the integrand is the probability that an immature survives unparasitized to size s (given that the adult parasitoid population remains fixed at the equilibrium level y_e). The expression $f(y_e)\psi(s)g(s)/y_e$ is the size specific (per immature host) parasitization rate per adult parasitoid (at equilibrium). The quantity $\pi(t_i)n(s)$ is the number of emergent parasitoids from an immature parasitized at size s and $1/g(s)$ is the expected time a host spends in size class s. Finally, $1/\delta$ is the expected life time of an adult parasitoid. Thus, $E(\psi)$ *is the (at equilibrium) expected number of parasitoid emergences per (immature) host of an adult parasitoid over the course of its life time.*

Since $\beta \int_{s_m}^{+\infty} x_e(s)\,ds$ is the rate of immature host production at equilibrium the identity (14) expresses the fact that at equilibrium the expected total number of parasitoid emergences of an adult parasitoid over the course of its life time must be 1, i.e. each parasitoid adult exactly replaces itself at population equilibrium.

From (14) we see that to choose $\psi(s)$ so that $\int_{s_m}^{+\infty} x_e(s)\,ds$ is minimized is the same as to choose $\psi(s)$ so that $E(\psi)$ is maximized. Thus, we arrive at the following result: *the parasitization preference distribution that minimizes the adult host population at equilibrium is the distribution that maximizes the expected number of parasitoid emergences per (immature) host of an adult parasitoid over the course of its life time.*

We will study the problem of determining the distribution ψ that maximizes $E(\psi)$ only to lowest order for β close to the critical bifurcation point β_{cr}. As $\beta \to \beta_{cr}$, we see from (11) that $y_e \to 0$. Thus,

$$E(\psi) = \frac{1}{\delta} \int_{s_b}^{s_m} \pi(t_i) n(s) f'(0)\psi(s) e^{-\int_{s_b}^{s} \mu(z)/g(z)\,dz}\,ds + O\left(|\beta - \beta_{cr}|\right).$$

To first order term in $\beta - \beta_{cr}$, $E(\psi)$ is maximized and the adult host population is minimized when

$$\int_{s_b}^{s_m} n(s)e^{-\int_{s_b}^{s} \mu(z)/g(z)dz}\psi(s)ds \tag{16}$$

is maximized. Our problem becomes: given n, g, and μ, what parasitization preference distribution ψ should the parasitoids use in order to maximize (16)?

Theorem 6 of the Appendix asserts that, in order to maximize (16), the parasitoids should attack only those size classes s at which

$$n(s)e^{-\int_{s_b}^{s} \mu(z)/g(z)dz} \tag{17}$$

attains a maximum as a function of $s \in [s_b, s_m]$. This quantity is the inherent (i.e. low parasitoid density) size-specific expected number of emerging adult parasitoids per host larva at equilibrium. Since the size classes are continuous rather than discrete, in most cases a continuous parasitization preference distribution function $\psi(s)$ will not maximize (16).

If (17) attains its maximum at only one size class, say $s = s_o \in [s_b, s_m]$, then Theorem 6 asserts that the parasitoids should attack only the size class s_o. (This is the conclusion reached for a general class of discrete models in [5].) In this case $\psi(s)$ must be taken as $\delta(s - s_o)$, the Dirac delta function located at s_o. It is, of course, impossible in this case for a continuous parasitization preference distribution $\psi(s)$ to maximize (16), although the parasitoids can come arbitrarily close to maximizing (16) by choosing a continuous preference distribution $\psi(s)$ sufficiently close to $\delta(s - s_o)$.

An example is given by the case when the number of emergents $n(s) = n$ is independent of the size s of the host victim, in which case (17) is clearly maximized at $s = s_b$. In this case only the smallest (newborn) immatures should be parasitized. (This is the conclusion reached in [1] for a class of discrete age-structured models.)

We summarize these results in the following theorem.

Theorem 3. *Assume $\beta_{cr} < \beta < \beta_{\infty}$. The parasitoids can come, to first order in $|\beta - \beta_{cr}|$, arbitrarily close to minimizing the adult host equilibrium level if and only if they concentrate sufficiently closely on those host size classes which maximize (17), the inherent (low parasitoid density) expected number of emerging adult parasitoids per host larva.*

4. Conclusions

In this paper we considered a continuous host-parasitoid model (2)–(3) for a size-structured host population that is parasitized in its immature stages. We are interested in the case when the host population grows exponentially in the absence of parasitization, i.e. $\beta_{cr} < \beta$. Theorem 2 implies that it is possible for the parasitoid to control the host population in the sense that a positive (coexistence) equilibrium state exists if $\beta_{cr} < \beta < \beta_\infty$. On the other hand, if the host population's growth rate is too large ($\beta > \beta_\infty$) then the parasitoid will fail to stop its exponential growth. By deriving the formula (12) for the adult host equilibrium level we determined that this equilibrium level is minimized by an appropriate choice of the parasitization preference distribution $\psi(s)$ if and only if the quantity $E(\psi)$ given by the formula (15) is maximized. The quantity $E(\psi)$ can be interpreted as the expected number of parasitoid emergences (per immature host) of an adult parasitoid over the course of its life time. For β sufficiently close to β_{cr} (i.e. for sufficiently small host exponential growth rates and for small parasitoid equilibrium levels) Theorem 3 characterizes the parasitization distribution $\psi(s)$ that (approximately) maximizes $E(\psi)$ and hence minimizes the adult host equilibrium level. Roughly speaking, this theorem says that the parasitization should be concentrated those host size classes which maximize the expression (17) as a function of s. This has the effect of maximizing the inherent (low parasitoid density) expected number of emerging adult parasitoids per host larva. These conclusions corroborate those reached in [5] by means of a discrete model. They also agree with Barclay's assertion that if size correlates exactly with chronological age ($g(s) \equiv 1$) and the number of parasitoid emergences from a host is a fixed constant (independent of host age), then the optimal strategy is to parasitize the youngest immature class and this class only.

There are several interesting unsolved problems associated with the model presented here. We have not studied the stability properties of the positive equilibria guaranteed by Theorem 2. The result in this Theorem can be viewed as a bifurcation phenomena as the parameter β is increased through the critical value β_{cr} at which the zero (extinction) equilibrium loses stability. Such a transcritical bifurcation is generally associated with an exchange of stability, which would led us to conjecture that the positive equilibria in Theorem 2 are locally asymptotically stable at least for β close to β_{cr}. However, because the host population in our model grows linearly in the absence of the parasites, this bifurcation is not "generic" and the formal bifurcation theorems do not apply.

Another interesting problem would be to investigate the robustness of the conclusions above (and in [1] and [5]) in models that include density dependence in the host population. Discrete models of this kind are considered numerically in [1].

Finally, a key unsolved problem is that of maximizing the nonlinear functional $E(\psi)$ over the set of normalized probability distributions ψ and determining the characteristics of the optimal distributions ψ.

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Appendix

$Q(t)$ denotes a proposition which depends on a real parameter t.

Theorem 4. [11] *Suppose $K \subseteq R$ is closed and bounded below in R; $A = \{t \in R \mid Q(t)$ is true$\}$ is open in R; and for all $t \in K$, $Q(t)$ is true whenever $Q(x)$ is true for all $x \in K$ such that $x < t$. Then $Q(t)$ is true for all $t \in K$.*

Proof. Suppose there is a $t \in K$ such that $Q(t)$ is not true. Then the set $(R-A) \cap K$ is nonempty, closed, and bounded below, and thus contains its infinum T. It follows that $Q(x)$ is true for all $x \in K$ such that $x < T$. Therefore, by assumption $Q(T)$ must be true. This is a contradiction and hence no such t can exist. $\square$

Theorem 5. *Let* $X = [a, b]$, $h \in C(X)$, $M = \max_{x \in X} \{h(x)\}$, $T : P(X) \to R$ *be defined by*

$$T(\mu) = \int_X h \, d\mu,$$

and $K = \{\mu \in P(X) \mid \int_X h \, d\mu = M\} = T^{-1}(M)$, *where* $P(X)$ *denotes the space of probability measures on* X. *Then* K *is the weak-star* ($wk - *$) *closure of*

$$\mathrm{co}\{\delta_x \mid x \in X \text{ and } h(x) = M\},$$

where the convex hull $\mathrm{co}\,A$ *of a set* A *is defined by*

$$\mathrm{co}\,A \doteq \{\sum_{i=1}^{n} a_i y_i \mid n \in N, \ a_i \in R^+, \ \sum_{i=1}^{n} a_i = 1, \ y_i \in A\}.$$

Proof. K is a convex set. We will begin by showing K is also $wk - *$ compact. It then follows from the Krein–Milman Theorem ([4], p. 142) that K is the $wk - *$ closure of $\mathrm{co}(\mathrm{ext}\,K)$, where $\mathrm{ext}\,K$ denotes the extreme points of K (points $y \in K$ such that no line segment containing y is contained in K). Finally we will prove that $\mathrm{ext}\,K = \{\delta_x \mid x \in X \text{ and } h(x) = M\}$.

(i) To show K is $wk - *$ compact we note, using the Riesz Representation Theorem, that $K \subseteq P(X) \subseteq \mathrm{ball}\,M(X) \cong \mathrm{ball}\,C_0(X)^* = \mathrm{ball}\,C(X)^*$ where $M(X)$ is the space of positive measures and $C_0(X)^*$ is the dual space of the space $C_0(X)$ of continuous functions on X which vanish at infinity. The set $\mathrm{ball}\,C(X)^*$ is $wk - *$ compact by Alaoglu's Theorem ([4], p. 130). Let $\{\mu_\alpha\} \subseteq K$ be a net which $wk - *$ converges to some $\mu \in \mathrm{ball}\,M(X)$. Now, $\mu_\alpha \to \mu$ ($wk - *$) if and only if $F_{\mu_\alpha} \to F_\mu$ pointwise in $C(X)^*$, which occurs if and only if for all $g \in C(X)$, $F_{\mu_\alpha}(g) \to F_\mu(g)$. The latter occurs if and only if for all $g \in C(X)$, $\int_X g \, d\mu_\alpha \to \int_X g \, d\mu$. Thus, $\int_X h \, d\mu_\alpha \to \int_X h \, d\mu$ which implies $\int_X h \, d\mu = M$. We need yet to show that $\mu \in P(X)$ (i.e. that μ is a positive measure). To see this, note that for each α, $\int_X g \, d\mu_\alpha \geq 0$ and hence $\int_X g \, d\mu \geq 0$ if $g \in C(X)$ is nonnegative. Thus, for all nonnegative $g \in C(X)$, $\int_X g \, d\mu \geq 0$. Let $H \subseteq X$ be compact. We can write the characteristic function χ_H as the limit of a decreasing nonnegative sequence of functions $\{g_n\} \subseteq C(X)$, and by the monotone convergence theorem,

$$\lim \int_X g_n \, d\mu = \int_X \chi_H \, d\mu = \int_H d\mu = \mu(H) \geq 0.$$

If E is a measurable set, then

$$\mu(E) = \sup\{\mu(H) \mid H \subseteq E \text{ and } H \text{ is compact}\} \geq 0.$$

Finally, $\mu(X) = 1$ since $\int_X d\mu_\alpha \to \int_X d\mu$. Therefore $\mu \in K$ and this completes the proof that K is $wk - *$ compact.

(ii) Finally we prove that $\text{ext } K = \{\delta_x \mid x \in X \text{ and } h(x) = M\}$. $K \neq \emptyset$ since there exists an $x \in X$ such that $h(x) = M$, and hence $\delta_x \in K$. Also, for all $\mu \in P(X)$, $T(\mu) \leq M$, and so M is an extreme point of $T[P(X)]$. By exercise 9, p. 145, and Theorem 8.4, p. 147 of [4], $\text{ext } K = \text{ext } T^{-1}(M) \subseteq \text{ext } P(X) = \{\delta_x \mid x \in X\}$. However, $\int_X h\,d\mu = h(x)$ for $\mu = \delta_x$ and so $\text{ext } K \subseteq \{\delta_x \mid x \in X \text{ and } h(x) = M\}$.

To show the reverse set containment, let $x_0 \in X$ such that $h(x_0) = M$. Clearly $\delta_{x_0} \in K$. Suppose $\chi, \psi \in K$ with $\delta_{x_0} = \frac{1}{2}(\chi + \psi)$. Then $\chi, \psi \in K \subseteq P(X)$ and $\delta_{x_0} \in \text{ext } P(X)$. Thus, $\chi = \psi = \delta_{x_0}$, and so $\delta_{x_0} \in \text{ext } K$. $\qquad\square$

Theorem 6. *Let $X = [a, b]$, $h \in C(X)$, $M = \max_{x \in X}\{h(x)\}$, and $E = \{x \in X \mid h(x) = M\}$. Let $\psi \in L^1(X)$ with $\int_a^b \psi(s)ds = 1$, and $\psi \geq 0$ on X. Then*

$$\int_a^b h(s)\psi(s)ds$$

is maximal if and only if $\text{supp } \psi \subseteq E$.

Proof. Suppose $\int_a^b h(s)\psi(s)ds$ is maximal. Define a measure μ by $\mu(A) = \int_A \psi\,ds$, so that $d\mu = \psi\,ds$. Then $\mu \in P(X)$. By Theorem 5, μ is in the $wk - *$ closure of $\text{co}\{\delta_x \mid x \in E\}$. Thus, there exists a net $\{\nu_\alpha\} \subseteq \text{co}\{\delta_x \mid x \in E\}$ of probability measures converging $wk - *$ to μ, and hence $\int_X g\,d\nu_\alpha \to \int_X g\,d\mu$ for all $g \in C(X)$. Let $y \in X - E$. Since E is closed in X, there exists an open neighborhood U of y such that $U \cap E = \emptyset$. Choose $p \in C(X)$ such that $p > 0$ on U and $p = 0$ on $X - U$. Then $p = 0$ on E and hence for all α it follows that $\int_X p\,d\nu_\alpha = 0$. This implies $\int_X p\,d\mu = 0$. Thus, $0 = \mu(U) = \int_U \psi(s)ds$, and so $\psi = 0$ on U; this implies that $y \notin \text{supp } \psi$, and we conclude $\text{supp } \psi \subseteq E$.

Conversely suppose $\text{supp } \psi \subseteq E$. Then $\int_a^b h(s)\psi(s)ds = \int_E h\,d\mu = M \int_E d\mu = M$. $\qquad\square$