MULTIPARASITOID-HOST INTERACTIONS WITH EGG-LIMITED ENCOUNTER RATES*

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Abstract. To address the contentious issue of multiple parasitoid introductions in classical biological control, a discrete-time model of multiparasitoid-host interactions that accounts for host density dependence and egg limitation is introduced and analyzed. For parasitoids that are egg limited but not search limited, the model is proven to exhibit four types of dynamics: host failure in which the host becomes extinct in the presence or absence of the parasitoids; parasitoid-driven extinction in which the parasitoid complex invariably drives the host extinct; host persistence; and conditional host persistence in which, depending on the initial ratios of host to parasitoid densities, the host is either driven extinct or persists. In the case of host persistence, the dynamics of the system are shown to be asymptotic to the dynamics of an appropriately defined one-dimensional difference equation. The results illustrate how the establishment of one or more parasitoids can facilitate the invasion of another parasitoid and how a complex of parasitoids can drive a host extinct despite every species in the complex being unable to do so. The effects of including search limitation are also explored.

Key words. host-parasitoid dynamics, permanence, extinction, Lyapunov exponents

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1. Introduction. Classical biological control is the introduction of natural enemies of a pest species with the goal of suppressing the abundance of the pest to a level at which it no longer causes economic damage [23]. For insect pests, control is often achieved by parasitoids: organisms, typically wasps and flies, whose young develop on and eventually kill their hosts. One of the earliest successes of biological control was with the cottony cushion scale, a pest that was devastating the developing California citrus industry in the late 1800s [4]. A predatory insect, the vedalia beetle (which functions as a parasitoid), and a parasitoid fly were introduced from Australia to control the cottony cushion scale. Within several years, these natural enemies suppressed this pest to very low densities, where they remain to this day when not disrupted by the use of broad-spectrum insecticides [23]. Since this pioneering project, there have been more than 3,600 intentional introductions of parasitoids to control more than 500 insect pests around the world [8]. Of these introductions, only 30% have resulted in the natural enemy establishing successfully, and of these only 36% have lead to substantial control of the targeted pest [8]. Consequently, there have been extensive theoretical and empirical efforts to understand what factors contribute to the success or failure of biological control programs. One particular contentious issue in these studies concerns whether or not the release of a single species or several species of natural enemy will lead to a lower host density. On the one hand, scientists have argued that it is essential to screen all natural enemies and release only the most effective species [32, 34, 5]. Others have argued that testing for the best

parasitoid species takes too much time and money and, consequently, have advocated releasing all available natural enemies [33, 15]. Theoretical studies have shown that whether multiple species introductions are advisable depends on the details of the biology [21, 18, 2, 29]. For instance, May and Hassell [21] argued that, in general, multiple parasitoid introductions result in greater suppression of the host than single parasitoid introductions. This conclusion, however, relied on the assumption that the parasitoid species aggregate independently of one another and independently of host density. Indeed, Kakehashi, Suzuki, and Iwasa [18] showed that single parasitoid introductions are more effective when both parasitoid species aggregate to the same regions of space. These theoretical studies assume that the parasitoids are search limited and not egg limited. Moreover, their analysis is typically limited to numerical simulations and, occasionally, equilibrium stability analysis. In contrast to these earlier studies, we analyze the global dynamics for multiparasitoid-host interactions when the parasitoids are egg limited but not search limited.

All parasitoids experience egg limitation to some degree [6, 12, 17, 19]. For instance, synovigenic parasitoids, which continuously produce eggs over their lifetime, experience egg limitation whenever the number of hosts they encounter in a day exceeds their daily production of eggs. In a field study, Heimpel and Rosenheim [12] caught and dissected 270 synovigenic parasitoids of the species *Aphelinidae aonidiae*. They found 18% of the dissected individuals had an egg load of zero and, consequently, were extremely egg limited. Several theoretical studies have examined the combined effects of egg limitation and search limitation on host-parasitoid dynamics [6, 10, 26, 30, 27, 28]. If one takes a broad view that egg limitation is a form of predator saturation, then it can be said that Rogers [26] was the first to consider egg limitation by translating Holling's type II functional response to a host encounter rate. Analyzing Roger's model, May and Hassell [10] found that egg limitation tends to destabilize host-parasitoid interactions. It was not until two decades later that the interaction of this destabilizing factor with a stabilizing factor (heterogeneity in the distribution of parasitoid attacks) was considered. Studying models without host self-regulation, Getz and Mills [6] found that stability of the host-parasitoid equilibrium requires parasitic attacks to be sufficiently aggregated and the intrinsic fitness of the parasitoid to exceed the intrinsic fitness of the host. Including host regulation, Schreiber found that parasitoids with aggregated attacks and sufficiently weak search limitation can suppress their hosts to extremely low densities and even drive them to extinction [27, 28]. None of these studies, however, considered how egg limitation influences multiparasitoid-host interactions. Given that classical biological control programs often involve the release of multiple parasitoid species, and that most parasitoids experience some degree of egg-limitation, an important facet of host-parasitoid dynamics remains to be understood.

To address this gap in our knowledge about host-parasitoid dynamics, we introduce and analyze a model of multiparasitoid-host interactions that accounts for egg-limitation. This model is presented in section 2. Using a simple change of variables introduced in [27], we provide in sections 3 and 4 a rather detailed analysis of the global dynamics for purely egg-limited parasitoids. In section 5, we examine the combined effects of weak search limitation and egg limitation. In section 6, we discuss the implications of our results for classical biological control.

2. Model. The discrete-time model describes the dynamics of host-parasitoid interactions with synchronized generations. The host of density N is subject to parasitism by n parasitoids of densities $P_1, \ldots, P_n$. The fraction $g_i(E_i)$ of hosts escaping

parasitism for species i depends on the host encounter rate E_i of parasitoid species i, a function of host and parasitoid density that is described in further detail below. The fraction of hosts escaping intraspecific density-dependent mortality is $f(N)$. Intraspecific density-dependent mortality is assumed to precede mortality due to parasitism (see, e.g., [13, 22, 27]). One interpretation of this assumption is that the parasitoids are koinobionts. Hence, the host continues to develop after being parasitized and experiences density-dependent mortality (via the survival function $f(\cdot)$) independent of parasitism. Hosts escaping parasitism and density-dependent mortality produce on average λ progeny that survive to the next generation. Following the approach taken by May and Hassell [21], we assume that there is a competitive hierarchy amongst parasitoid larvae: within a parasitized host, larvae from species i always outcompete larvae from species j whenever $j > i$. This assumption is appropriate for two types of interactions that are frequently found in host-parasitoid systems [21]. First, it applies when parasitoid species 1 attacks first, species 2 attacks second, etc. In these cases, the older parasitoid larvae are usually able to eliminate the younger competitors by physical suppression [7]. This situation is common when the parasitoid species attack different developmental stages of the host, e.g., parasitoid 1 attacks the egg stage while parasitoid 2 attacks the larval or pupal stage. Second, the assumption can also apply when the parasitoids attack the same stage of the host but exhibit a competitive hierarchy. For instance, Chow and Mackauer [3] studied multiple parasitism of the pea aphid by the solitary hymenopterous parasites *Aphidius smithi* and *Praon pequodorum* in the laboratory. They found in larval competition, *P. pequodorum* was intrinsically superior to *A. smithi*, regardless of the latter's age. Finally, we assume that, on average, θ_i parasitoids emerge from a host parasitized by species i. Under these assumptions, the model is given by

(2.1)
$$
\begin{cases}
N' &= \lambda f(N)N g_1(E_1) g_2(E_2) \cdots g_n(E_n), \\
P_1' &= \theta_1 f(N)N \{1 - g_1(E_1)\}, \\
P_2' &= \theta_2 f(N)N g_1(E_1)\{1 - g_2(E_2)\}, \\
&\vdots \\
P_n' &= \theta_n f(N)N g_1(E_1) \cdots g_{n-1}(E_{n-1})\{1 - g_n(E_n)\},
\end{cases}
$$

where N' and P_i' are the densities of the host and parasitoids, respectively, in the next generation. The state space for the host-parasitoid dynamics is $\mathbf{R}_+^{n+1} = \{(N, P) \in \mathbf{R} \times \mathbf{R}^n : N \geq 0, P_i \geq 0 \text{ for all } i\}$.

To complete the model, it is necessary to specify the density-dependent survivorship function $f(N)$, the encounter rate function E, and the escape functions g_i. Throughout this article, we assume the following:

A1. f is a continuous decreasing positive function such that $f(0) = 1$ and $\lim_{N \to \infty} f(N) = 0$.

Survivorship functions that satisfy assumption A1 include the generalized Beverton–Holt function $f(N) = \frac{1}{1+\alpha N^\beta}$ with $\alpha > 0$ and $\beta > 0$, the Ricker function $f(N) = \exp(-\alpha N)$ with $\alpha > 0$, and the Hassell function $f(N) = \frac{1}{(1+\alpha N)^\beta}$. To simultaneously account for search limitation and egg limitation, we follow the approach of Rogers [26] and define the average host encounter rate as

$$
E_i = \frac{\alpha_i P_i}{1 + \alpha_i b_i N},
$$

where α is the searching efficiency of the parasitoid and b_i corresponds to the handling time or egg limitation of the parasitoid. For parsimony, we rewrite this average

encounter rate as

$$(2.2) \qquad E = \frac{P_i}{a_i + b_i N},$$

where $a_i = \frac{1}{\alpha_i}$. One can view a_i as a measurement of search limitation. When there is no egg limitation (i.e., $b_i = 0$), the encounter rate reduces to the classical Nicholson–Bailey search limited encounter rate of $E_i = P_i/a_i$. Alternatively, when there is no search limitation (i.e., $a_i = 0$), the encounter rate reduces to the Thompson model $E_i = P_i/(b_i N)$ of egg-limited encounter rates [27, 31]. If eggs are randomly laid on hosts, then the fraction of hosts escaping parasitism is $\exp(-E_i)$. More generally, the Poisson escape term $\exp(-E_i)$ can be viewed as a limiting case of the negative binomial escape term $(1+E_i/k_i)^{-k_i}$ as $k_i \uparrow \infty$. This negative binomial escape function is commonly used to model nonrandom or aggregated parasitism events [6, 9, 13, 20]. In particular, $1/k_i$ can be interpreted as the coefficient of variation squared (CV^2) of the host encounter rate [11]. Consequently, larger values of k_i correspond to parasitic attacks being more evenly distributed across the hosts, while smaller values of k_i correspond to parasitoid attacks being aggregated on fewer hosts. To allow for this continuum of possibilities, we assume the following:

A2. $g_i(E_i) = \left(1 + \frac{E_i}{k_i}\right)^{-k_i}$ and $E_i = \frac{P_i}{a_i + b_i N_i}$ with $k_i > 0$ (possibly ∞), $a_i \geq 0$, and $b_i \geq 0$.

For ease of exposition, we write $k_i = \infty$ to refer to the Poisson escape function. The most important feature of escape function for the analysis is that $1/g_i$ is a concave function when $k_i < 1$ and $1/g_i$ is a convex function when $k_i > 1$.

Finally, to keep things meaningful, we assume the following:

A3. $\lambda, \theta_1, \ldots, \theta_n > 0$.

3. Egg-limited dynamics. Throughout this section, we assume that $a_i = 0$; i.e., there is no search limitation. For this case, we can make the change of variables

$$x = N, y_1 = E_1 = \frac{P_1}{b_1 N}, \ldots, y_n = E_n = \frac{P_n}{b_n N},$$

for which the dynamics of (2.1) partially decouple as follows:

$$(3.1) \qquad
\begin{cases}
x' &= \lambda f(x) x g_1(y_1) g_2(y_2) \cdots g_n(y_n), \\[2mm]
y_1' &= \frac{\theta_1}{b_1 \lambda}\left(\frac{1}{g_1(y_1)} - 1\right)\frac{1}{g_2(y_2)}\frac{1}{g_3(y_3)} \cdots \frac{1}{g_n(y_n)}, \\[2mm]
y_2' &= \frac{\theta_2}{b_2 \lambda}\left(\frac{1}{g_2(y_2)} - 1\right)\frac{1}{g_3(y_3)} \cdots \frac{1}{g_n(y_n)}, \\[1mm]
&\vdots \\[1mm]
y_{n-1}' &= \frac{\theta_{n-1}}{b_{n-1}\lambda}\left(\frac{1}{g_{n-1}(y_{n-1})} - 1\right)\frac{1}{g_n(y_n)}, \\[2mm]
y_n' &= \frac{\theta_n}{b_n \lambda}\left(\frac{1}{g_n(y_n)} - 1\right).
\end{cases}$$

To state our main result for this system, we need the following definition. Note that each $\frac{1}{g_i(y_i)} - 1$ is an increasing and strictly convex or concave function through the origin under assumption A2 and $k_i \neq 1$. Consequently, the nonnegative y_i^* defined below exist.

DEFINITION 3.1. *Assume* A2, A3, *and* $k_i \neq 1$ *for all* i. *Let* $C = \{i : k_i > 1\}$. *Define* y_n^* *to be the largest root of* $y_n = \frac{\theta_n}{b_n \lambda}\left(\frac{1}{g_n(y_n)} - 1\right)$. *Assuming* y_j^* *is defined for*

$j = i + 1, \ldots, n$, *define y_i^* to be the largest root of*

$$y_i = \frac{\theta_i}{b_i \lambda} \left(\frac{1}{g_i(y_i)} - 1 \right) \frac{1}{g_{i+1}(\hat{y}_{i+1})} \cdots \frac{1}{g_n(\hat{y}_n)},$$

where

$$\hat{y}_j = \begin{cases} 0 & if \ j \in C, \\ y_j^* & if \ j \notin C. \end{cases}$$

Our main result is the following theorem. A key quantity in this theorem is $\lambda g_1(y_1) \ldots g_n(y_n)$, which corresponds to the expected number of progeny produced per host.

THEOREM 3.2. *Assume* A1–A3, $k_i \neq 1$ *for all i, $a_i = 0$ for all i, $\theta_i \neq b_i \lambda \prod_{j=i+1}^{n} g_j(\hat{y}_j)$ for $1 \leq i \leq n - 1$, and $\theta_n \neq b_n \lambda$. Let $C = \{i : k_i > 1\}$. Then we have the following:*

Host extinction. *If $y_i^* = 0$ for some $i \in C$, or $y_i^* > 0$ for all $i \in C$ (possibly $C = \emptyset$) and $\lambda g_1(\hat{y}_1) \ldots g_n(\hat{y}_n) < 1$, then*

$$\lim_{t \to \infty} (N(t), P_1(t), \ldots, P_n(t)) = (0, 0, \ldots, 0)$$

whenever $N(0) \prod_{i=1}^{n} P_i(0) > 0$.

Host persistence. *If $C = \emptyset$ and $\lambda g_1(y_1^*) \ldots g_n(y_n^*) > 1$, then there exists a positive constant $\delta > 0$ such that*

$$\liminf_{t \to \infty} N(t) \geq \delta \quad and \quad \lim_{t \to \infty} \frac{P_i(t)}{b_i N(t)} = y_i^*$$

for all i whenever $N(0) \prod_{i=1}^{n} P_i(0) > 0$.

Conditional extinction. *If $y_i^* > 0$ for all $i \in C$, $C \neq \emptyset$, and $\lambda g_1(\hat{y}_1) \ldots g_n(\hat{y}_n) > 1$, then there exist Borel sets $U, V \subset \mathbf{R}_+^{n+1}$ and $\delta > 0$ such that*

$$\liminf_{t \to \infty} N(t) \geq \delta, \qquad \lim_{t \to \infty} \prod_{i=1}^{n} P_i(t) = 0$$

whenever $(N(0), P_1(0), \ldots, P_n(0)) \in U$, and

$$\lim_{t \to \infty} (N(t), P_1(t), \ldots, P_n(t)) = (0, 0, \ldots, 0)$$

whenever $(N(0), P_1(0), \ldots, P_n(0)) \in V$. Moreover, U has positive (possibly infinite) Lebesgue measure, V has infinite Lebesgue measure, and $\mathbf{R}_+^{n+1} \setminus (U \cup V)$ has Lebesgue measure zero.

Theorem 3.2 (modulo equalities) characterizes the persistence and extinction dynamics of (2.1). In particular, host extinction can occur in two ways. If the host intrinsic fitness λ is less than one, then the host is unable to sustain itself and becomes extinct. Alternatively if $\lambda > 1$, then the host can persist in the absence of the parasitoids. However, if either $k_i > 1$ and $y_i^* = 0$ for a parasitoid or $\lambda \prod_{i=1}^{n} g_i(\hat{y}_i) < 1$, then the parasitoids drive the host extinct. Unconditional persistence of the host can occur only if the parasitoid attacks are sufficiently aggregated (i.e., $k_i < 1$ for all i) and the parasitoids do not overexploit their host (i.e., $\lambda \prod_{i=1}^{n} g_i(y_i^*) > 1$). How these different outcomes depend on the degree of egg limitation is illustrated in Figure 3.1
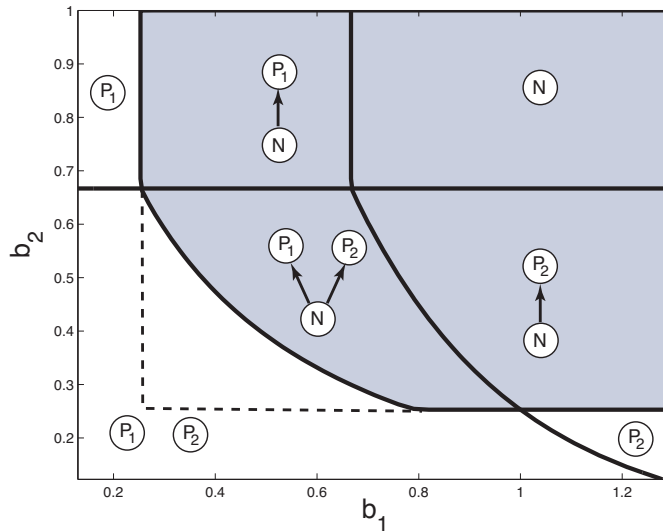
FIG. 3.1. *Ecological outcomes and how they vary with egg limitation. There are two parasitoids with conversion efficiencies $\theta_i = 1$ and aggregation parameters $k_i = 0.2$. The intrinsic fitness of the host is $\lambda = 1.5$. In the shaded region, the species that persist are shown. In the unshaded region, the host is driven to extinction by the indicated parasitoid(s). The dashed line delineates the region where both parasitoids but not a single parasitoid can drive the host to extinction.*

for parasitoids whose attacks are sufficiently aggregated. When egg limitation is sufficiently severe (i.e., b_i is sufficiently large) for a parasitoid species, the parasitoid is unable to establish itself. When egg limitation is sufficiently weak for a parasitoid species, it drives the host extinct. At intermediate levels of egg limitation, multiple parasitoids can drive the host to extinction when a single parasitoid species cannot (Figure 3.2 with parameter values from the dashed region in Figure 3.1).

When parasitoid attacks are sufficiently aggregated (i.e., $k_i < 1$ for all i), our results imply that the host dynamics have the limiting equation

$$N' = \lambda f(N) N \prod_{i=1}^{n} g_i(y_i^*),$$

and the parasitoid dynamics track the host dynamics; i.e., asymptotically the ratio of the parasitoid to the host approaches $b_i y_i^*$ for parasitoid species i. Consequently, in this case a lot more can be said about the dynamics provided that the dynamics of the host are well understood. For instance, when the host dynamics can be described by the Beverton–Holt model, we get the following corollary of Theorem 3.2.

COROLLARY 3.3. *Suppose that $f(N) = \frac{1}{1+\alpha N}$, $k_i < 1$ for all i, and $\lambda^* := \lambda \prod_{i=1}^{n} g_i(y_i^*) > 1$. Then*

$$\lim_{t \to \infty} N(t) = \frac{\lambda^* - 1}{\alpha}, \qquad \lim_{t \to \infty} P_i(t) = \frac{b_i y_i^*(\lambda^* - 1)}{\alpha}$$

whenever $N(0) \prod_{i=1}^{n} P_i(0) > 0$.

Proof. Since $k_i < 1$ for all i and $\lambda^* > 1$, the second assertion of Theorem 3.2 applies. Let $Z(t) = (N(t), P_1(t), \ldots, P_n(t))$ be a solution with $N(0) \prod_{i=1}^{n} P_i(0) > 0$.
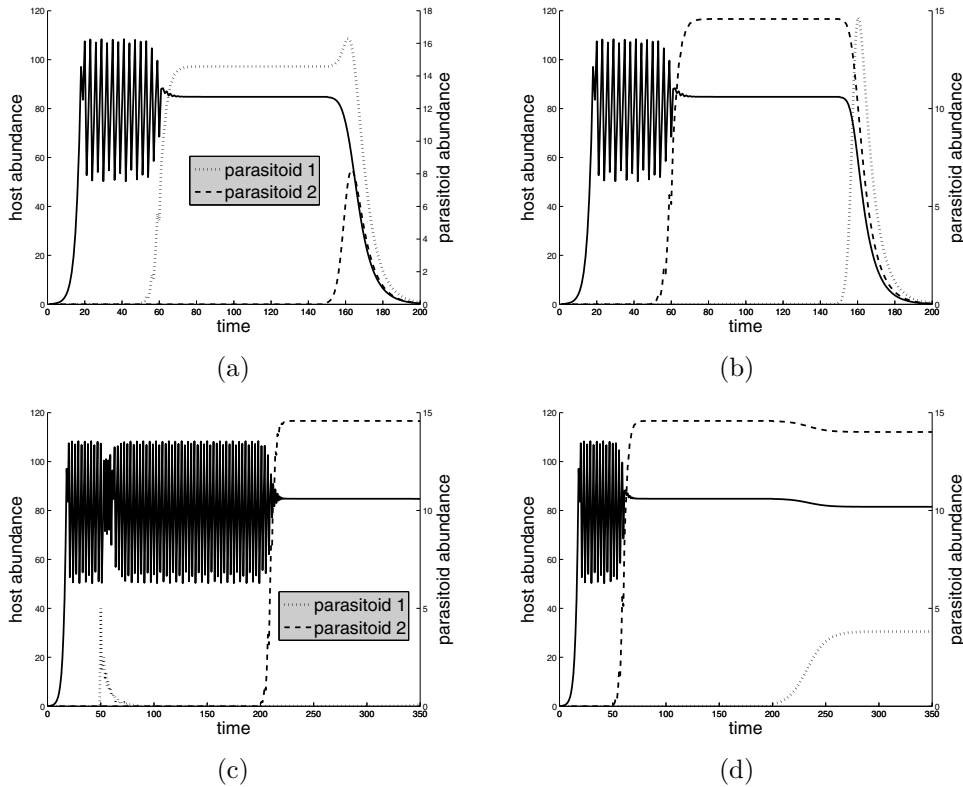
FIG. 3.2. *The effect of introducing one parasitoid at a time on the host-parasitoid dynamics. In* (a) *and* (c), *parasitoid* 1 *is introduced first, while parasitoid* 2 *is introduced later. In* (b) *and* (d), *the introduction order of parasitoids is reversed. In* (a) *and* (b), *the host is driven extinct only when both parasitoids are present. In* (c) *and* (d), *parasitoid* 1 *can establish itself only after parasitoid* 2 *has been established. In all figures,* $\lambda = 1.5$, $k_i = 0.2$, $f(N) = 1/(1 + (0.01N)^{10})$, *and* $\theta_i = 1.0$. *In* (a) *and* (b), $b_1 = b_2 = 0.4$. *In* (c) *and* (d), $b_1 = 0.75$ *and* $b_2 = 0.4$.

A result of Robinson [25] implies that the ω-limit set of $Z(t)$ is a chain recurrent set (see [25] for a definition). Theorem 3.2 implies that $\lim_{t\to\infty} \frac{P_i(t)}{N(t)} = b_i y_i^*$ for all i and $\liminf_{t\to\infty} N(t) > 0$. Since the only chain recurrent set in the invariant ray $\{(\eta, b_1 y_1^* \eta, \ldots, b_n y_n^* \eta) : \eta > 0\}$ is the equilibrium $\frac{\lambda^*-1}{\alpha}(1, y_1^* b_1, \ldots, y_n^* b_n)$, the corollary follows.   ∎

4. Proof of Theorem 3.2. We begin with a lemma that shows that (2.1) is dissipative.

LEMMA 4.1. *Assume* A1–A3. *There exists a constant* $M > 0$ *such that*

$$\limsup_{t\to\infty} N(t) \le M, \qquad \limsup_{t\to\infty} P_i(t) \le M$$

for all solutions $(N(t), P_1(t), \ldots, P_n(t))$ *to* (2.1).

Proof. Assumption A1 implies that there exists $M_1 > 0$ such that $\lambda f(x) < 0.9$ for all $x \ge M_1$. Define $M_2 = \max\{M_1, \lambda M_1\}$ and

$$M = \max\{M_2, \theta_1 M_2, \ldots, \theta_n M_2\}.$$

Let $(N(t), P_1(t), \ldots, P_n(t))$ be a solution to (2.1). First, we will show that there exists a $T \geq 0$ such that $N(T) \leq M_2$. If $N(0) \leq M_2$, then we are done. Suppose $N(0), \ldots, N(t) > M_2$. Since $g_1 \leq 1, \ldots, g_n \leq 1$, f is decreasing, and $M_2 \geq M_1$, it follows that

$$N(t) = \lambda f(N(t-1))N(t-1)g_1(y_1(t-1)) \ldots g_n(y_n(t-1)) \leq 0.9N(t-1).$$

Induction implies that $N(t) \leq 0.9^t N(0)$. Therefore, there exists $T \geq 0$ such that $N(T) \leq M_2$. Next, suppose that $N(T), \ldots, N(T+t) \leq M_2$. Since $g_1 \leq 1, \ldots, g_n \leq 1$, and f is decreasing, $N(T+t+1) \leq 0.9N(T+t) \leq 0.9M_2$ if $N(T+t) \geq M_1$, else $N(T+t+1) \leq \lambda M_1 \leq M_2$. Hence, induction implies that $N(t) \leq M_2 \leq M$ for all $t \geq T$. Finally, since $f \leq 1$ and $g_i \in [0, 1]$ for $1 \leq i \leq n$,

$$P_i(t+1) \leq \theta_i N(t) \leq \theta_i M_2 \leq M$$

for all $t \geq T$.   □

Define

$$G_i(y_i) = \frac{\theta_i}{b_i \lambda}\left(\frac{1}{g_i(y_i)} - 1\right).$$

LEMMA 4.2. *Assume* A2, A3, *and* $k_i \neq 1$. *Then*

$$z_i = c\, G_i(z_i) \tag{4.1}$$

has a nonnegative root for every $c \geq 0$. *For every* $c \geq 0$ *define* $z_i^*(c)$ *by the largest root of* (4.1). *Then the function* $z_i^* : \mathbf{R}_+ \to \mathbf{R}_+$ *is continuous.*

Proof. Since $0 = c\, G_i(0)$, $z_i = 0$ is always a root of (4.1). The function G_i is increasing and either strictly concave or strictly convex. Therefore, (4.1) has at most one positive root. This fact implies that z_i^* is a nonnegative function of c.

Consider the case where the function G_i is strictly concave, i.e., $k_i < 1$. In this case, (4.1) has a unique positive root if and only if $c > 1/G_i'(0)$. Therefore, $z_i^*(c) = 0$ if $c \in [0, 1/G_i'(0)]$ and $z_i^*(c) > 0$ if $c \in (1/G_i'(0), \infty)$. Since $z_i^*(c)$ is clearly continuous in $[0, 1/G_i'(0))$, it remains to show its continuity in $[1/G_i'(0), \infty)$. Define

$$F(c, z_i) = \begin{cases} 1 - cG_i'(0) & \text{if } z_i = 0, \\ 1 - cG_i(z_i)/z_i & \text{if } z_i > 0. \end{cases}$$

Then, by definition, $F(c, z_i^*(c)) = 0$ for all $c \in [1/G_i'(0), \infty)$. Furthermore, we can show that for each $c \in [1/G_i'(0), \infty)$,

$$\frac{\partial F}{\partial z_i} = \begin{cases} \frac{c\theta_i(1-k_i)}{2\lambda b_i k_i} \neq 0 & \text{if } z_i = 0, \\ \frac{c\theta_i}{\lambda b_i z_i^2}\left\{\left(1 + \frac{1-k_i}{k_i}z_i\right)\left(1 + \frac{z_i}{k_i}\right)^{k_i-1} - 1\right\} \neq 0 & \text{if } z_i > 0. \end{cases}$$

Thus the application of the implicit function theorem to $F(c, z) = 0$ at $(c^*, z_i(c^*))$ with $c^* \in [1/G_i'(0), \infty)$ implies that there exists a continuous function $h(c)$ such that $F(c, h(c)) = 0$ holds in a neighborhood of $(c^*, z_i^*(c^*))$. Since a positive root of (4.1) is unique, h and z_i^* must be identical. The arbitrariness of c^* implies that $z_i^*(c)$ is continuous.

The case $k_i > 1$ can be proved similarly. In this case, (4.1) has a unique positive root if and only if $c\,G_i'(0) < 1$. □

LEMMA 4.3. *Assume* A2–A3 *and* $k_i \neq 1$. *Let* $z_i^*(c)$ *be the same as in Lemma* 4.2, *and let* $y_i(t)$ *be a solution to*

$$y_i(t+1) = G_i(y_i(t))c(t),$$

where $c(t)$ *is a positive sequence with* $\liminf_{t \to \infty} c(t) = \underline{c}$ *and* $\limsup_{t \to \infty} c(t) = \overline{c}$. *If* $k_i < 1$, *then*

$$z_i^*(\overline{c}) \geq \limsup_{t \to \infty} y_i(t) \geq \liminf_{t \to \infty} y_i(t) \geq z_i^*(\underline{c}).$$

If $k_i > 1$ *and* $\overline{c} = \underline{c}$, *then either*

$$\lim_{t \to \infty} y_i(t) = \infty, \ \lim_{t \to \infty} y_i(t) = z_i^*(\underline{c}) \ \text{or} \ \lim_{t \to \infty} y_i(t) = 0.$$

Proof. Suppose that $k_i < 1$. By assumption, for each $\epsilon > 0$ there exists a $T \geq 0$ such that

$$G_i(y_i(t))(\overline{c} + \epsilon) \geq y_i(t+1) \geq G_i(y_i(t))(\underline{c} - \epsilon)$$

for all $t \geq T$. Let $z(t)$ and $w(t)$ be the solutions of

$$z(t+1) = G_i(z(t))(\underline{c} - \epsilon) \ \text{and} \ w(t+1) = G_i(w(t))(\overline{c} + \epsilon)$$

with $z(T) = w(T) = y_i(T)$. Then, by the monotonicity of G_i, $w(t) \geq y_i(t) \geq z(t)$ holds for all $t \geq T$. Since G_i is concave and $\lim_{x \to \infty} G_i(x)/x = 0$, it follows that $\lim_{t \to \infty} z(t) = z_i^*(\underline{c} - \epsilon)$ and $\lim_{t \to \infty} w(t) = z_i^*(\overline{c} + \epsilon)$. Therefore, we have

$$z_i^*(\overline{c} + \epsilon) \geq \limsup_{t \to \infty} y_i(t) \geq \liminf_{t \to \infty} y_i(t) \geq z_i^*(\underline{c} - \epsilon).$$

Since $\epsilon > 0$ is arbitrary and $z_i^*(c)$ is a continuous function, this inequality implies the first statement of the lemma.

Suppose that $k_i > 1$ and $\underline{c} = \overline{c}$. Suppose that $\limsup_{t \to \infty} y_i(t) < \infty$. Then the limit set of $y_i(t)$ is a compact internally chain recurrent set (see, e.g., [1]) for the dynamics of $y_i' = G_i(y_i)\underline{c}$. Since the only internally chain recurrent sets are the equilibria, 0, and $z_i^*(\underline{c})$ (possibly also 0), $\lim_{t \to \infty} y_i(t) = 0$ or $\lim_{t \to \infty} y_i(t) = z_i^*(\underline{c})$. Suppose that $\limsup_{t \to \infty} y_i(t) = \infty$. Since $\lim_{x \to \infty} G_i(x)/x = \infty$ (as $k_i > 1$) and G_i is convex, there exists $T > 0$, $M > 0$, and $\epsilon > 0$ such that

$$G_i(x)c(t) \geq (1 + \epsilon)x$$

for all $t \geq T$ and $x \geq M$. Choose $T_2 > T$ such that $y_i(T_2) \geq M$. Then $y_i(T_2 + t) \geq (1 + \epsilon)^t y_i(T_2)$ for all $t \geq 0$. Hence, $\lim_{t \to \infty} y_i(t) = \infty$. □

Let $(x(t), y_1(t), \ldots, y_n(t))$ be a positive solution to (3.1). An important implication of Lemma 4.3 is that $\liminf_{t \to \infty} y_i(t) \geq \hat{y}_i$. Indeed, Lemma 4.3 with $c(t) = 1$ applied to $y_n(t)$ implies $\liminf_{t \to \infty} y_n(t) \geq \hat{y}_n$. Suppose that $\liminf_{t \to \infty} y_i(t) \geq \hat{y}_i$ for $i = j + 1, \ldots, n$. To prove the assertion for $i = j$, consider two cases. If $k_j > 1$, then $\hat{y}_j = 0$ and the assertion holds. If $k_j < 1$, then apply Lemma 4.3 with $c(t) = \prod_{i=j+1}^{n} 1/g_i(y_i(t))$.

To prove the first assertion of Theorem 3.2 about unconditional host extinction, we consider two cases. First, suppose that $y_i^* = 0$ for some $i \in C$. Then $G_i'(0)\hat{c} > 1$, where $\hat{c} = \frac{1}{g_{i+1}(\hat{y}_{i+1})} \cdots \frac{1}{g_n(\hat{y}_n)}$. Since $\liminf_{t\to\infty} y_j(t) \geq \hat{y}_j$ for all $i + 1 \leq j \leq n$, continuity and monotonicity of g_j for $i \leq j \leq n$ imply that there exists a $T \geq 0$ and an $\eta > 1$ such that $y_i(t+1) \geq \eta y_i(t)$ for all $t \geq T$. Hence, $\lim_{t\to\infty} y_i(t) = \infty$. Since $P_i(t)$ is bounded by Lemma 4.1, it follows that $\lim_{t\to\infty} x(t) = 0$. For the second case, we assume that $y_i^* > 0$ for all $i \in C$ and $\lambda f(0)g_1(\hat{y}_1)\cdots g_n(\hat{y}_n) < 1$. Since $\liminf_{t\to\infty} y_i(t) \geq \hat{y}_i$ for all i and g_i are decreasing functions, there exist constants $\lambda_M < 1$ and $T \geq 0$ such that $\lambda f(0)g_1(y_1(t))\cdots g_n(y_n(t)) \leq \lambda_M$ for all $t \geq T$. Therefore, $x(t+1) \leq \lambda_M x(t)$ holds for all $t \geq T$. Hence $\lim_{t\to\infty} x(t) = 0$.

To prove the second assertion of Theorem 3.2 about unconditional host persistence, assume that $C = \emptyset$ and $\lambda f(0)g_1(y_1^*)\cdots g_n(y_n^*) > 1$. Applying Lemma 4.3 inductively to $y_i(t)$ with $c(t) = \prod_{j=i+1}^n 1/g_j(y_j(t))$ implies that $\lim_{t\to\infty} y_i(t) = \hat{y}_i = y_i^*$ for all i. By the continuity of g_i, there exist $\lambda_M \geq \lambda_m > 1$ and $T_1 \geq 0$ such that

$$\lambda g_1(y_1(t))\cdots g_n(y_n(t)) \in [\lambda_m, \lambda_M]$$

for all $t \geq T_1$. Since f is continuous, we can choose $\delta > 0$ such that $\lambda_m f(x) > 1$ for $x \in [0, \delta]$. Define $\alpha = \inf\{\lambda_m f(x)x : x > \delta\}$. Suppose $\alpha > 0$. Let $m = \min\{\delta, \alpha\}$. Since $\lambda_m f(x)x > x$ for all $x \in (0, m)$, there exists $T_2 \geq T_1$ such that $x(T_2) \in [m, \infty)$. By the definition of m, x does not escape from the interval (m, ∞). Finally, suppose $\alpha = 0$. Since $\lambda_M f(x) > 1$ for all $x \in [0, \delta]$ and $\lambda_M f(x) < 1$ for some $x > \delta$, the continuity of f ensures that the equation $\lambda_M f(x) = 1$ has a positive solution in the interval (δ, ∞). Since f is decreasing, there exists a unique positive solution, say $\bar{x} \in (\delta, \infty)$. Let $M = \max\{\lambda_M f(x)x : x \in [0, \bar{x}]\}$ and $\beta = \min\{\lambda_m f(x)x : x \in [\delta, M]\}$. Define $m = \min\{\delta, \beta\}$. By the definitions of m and M, if $x(t) \in [m, M]$ for some $t \geq T_1$, then $x(t)$ does not escape from the interval $[m, M]$. If $x(T_1) \in (M, \infty)$, then either $x(t) \in (M, \infty)$ for all $t \geq T_1$ or $x(T_2) \in (0, M]$ for some $T_2 \geq T_1$. Since the former case provides the desired conclusion, we consider the latter case. On the interval $(0, m)$, $\lambda_m f(x)x > x$ holds. Therefore, there exists a $T_3 \geq T_2$ such that $x(T_3) \in [m, M]$. This completes the proof of the second assertion of the theorem.

To prove the final assertion of Theorem 3.2, assume that $y_i^* > 0$ for all $i \in C$, $C \neq \emptyset$, and $\lambda g_1(\hat{y}_1)\ldots g_n(\hat{y}_n) > 1$. Assume $C = \{i_1, \ldots, i_k\}$ with $i_1 > i_2 > \cdots > i_k$. For each $1 \leq j \leq n$, define $U(j)$ as the set of initial conditions $(N(0), P_1(0), \ldots, P_n(0)) \in \mathbf{R}_+^{n+1}$ such that

$$N(0)\prod_{i=1}^n P_i(0) > 0 \text{ and } \lim_{t\to\infty} y_i(t) = \hat{y}_i \text{ for all } i \geq j,$$

and define $V(j)$ as the set of initial conditions such that

$$N(0)\prod_{i=1}^n P_i(0) > 0 \text{ and } \lim_{t\to\infty} y_i(t) = \infty \text{ for some } i \geq j.$$

For $j = i_1, i_2, \ldots, i_k$, we will prove inductively that $\mathbf{R}_+^{n+1} \setminus (U(j) \cup V(j))$ has Lebesgue measure zero.

As the first step of the induction, let $j = i_1$. If $j = n$, then convexity of G_n implies that $\lim_{t\to\infty} y_n(t) = \infty$ whenever $y_n(0) > y_n^*$, $y_n(t) = y_n^*$ for all t whenever $y_n(0) = y_n^*$, and $\lim_{t\to\infty} y_n(t) = 0$ whenever $y_n(0) < y_n^*$. Hence, $\mathbf{R}^{n+1} \setminus (U(j) \cup V(j))$ has Lebesgue measure zero. Assume that $j < n$. Since $k_i < 1$ for $i > j$, applying Lemma 4.3

inductively to $i = n, n-1, \ldots, j+1$ with $c(t) = 1, 1/g_n(y_n(t)), \ldots, \prod_{i=j+2}^{n} 1/g_i(y_i(t))$ implies that $\lim_{t \to \infty} y_i(t) = y_i^*$ for $i > j$ whenever $y_i(0) > 0$ for $i > j$. Applying Lemma 4.3 to $i = j$ with $c(t) = \prod_{i>j} 1/g_i(y_i(t))$ implies that either

$$\lim_{t \to \infty} y_j(t) = \hat{y}_j = 0, \ \lim_{t \to \infty} y_j(t) = y_j^*, \ \text{or} \ \lim_{t \to \infty} y_j(t) = \infty.$$

The derivative of $y_j', \ldots, y_n'$ in (3.1) with respect to $y_j, \ldots, y_n$ is an upper triangular matrix whose diagonal elements are given by $d_i(y_i, \ldots, y_n) = G_i'(y_i) \prod_{l=i+1}^{n} 1/g_l(y_l)$ for $i = j, \ldots, n$. Since G_i are concave for $i = j+1, \ldots, n$, G_j is convex, and $\theta_i \neq b_i \lambda \prod_{l=i+1}^{n} g_l(\hat{y}_l)$ for $1 \leq i \leq n$, it follows that $d_i(\hat{y}_i, \ldots, \hat{y}_n) < 1$ for $i > j$ and $d_j(y_j^*, \hat{y}_{j+1}, \ldots, \hat{y}_n) > 1$. Hence, $(y_j^*, \hat{y}_{j+1}, \ldots, \hat{y}_n)$ is a hyperbolic equilibrium for the dynamics of (3.1) restricted to the $y_j, \ldots, y_n$ subsystem. Moreover, the stable manifold of this equilibrium has codimension one in the $y_j, \ldots, y_n$ hyperplane. Since the local stable manifold has Lebesque measure zero, and $y_j', \ldots, y_n'$ in (3.1) is a diffeomorphism, the global stable manifold which is a countable union of preimages of the local stable manifold also has Lebesgue measure zero. Thus, $\mathbf{R}_+^{n+1} \setminus (U(j) \cup V(j))$ has Lebesgue measure zero.

For the next step of the induction, assume that $\mathbf{R}_+^{n+1} \setminus (U(j) \cup V(j))$ has Lebesgue measure zero for $j = i_1, \ldots, i_l$. Let $j = i_{l+1}$. Suppose that $\lim_{t \to \infty} y_i(t) = \hat{y}_i$ for all $i \geq i_l$, i.e., $(N(0), P_1(0), \ldots, P_n(0)) \in U(i_l)$. Since $k_i < 1$ for $i_{l+1} < i < i_l$, Lemma 4.3 applied inductively implies that $\lim_{t \to \infty} y_i(t) = \hat{y}_i$ for $i_{l+1} < i < i_l$, and consequently, $\lim_{t \to \infty} y_i(t) = \hat{y}_i$ for $i > i_{l+1}$. Since $k_j > 1$, Lemma 4.3 implies that either

$$\lim_{t \to \infty} y_j(t) = 0, \ \lim_{t \to \infty} y_j(t) = y_j^*, \ \text{or} \ \lim_{t \to \infty} y_j(t) = \infty$$

Using an argument similar to the first step of the induction, the equilibrium $(y_j^*, \hat{y}_{j+1}, \ldots, \hat{y}_n)$ is a hyperbolic equilibrium for the dynamics of (3.1) restricted to the $y_j, \ldots, y_n$ hyperplane. Moreover, the stable manifold of this equilibrium has codimension greater than or equal to one. Hence, $U(i_l) \setminus (U(j) \cup V(j))$ has Lebesgue measure zero. Since $V(i_l) \subset V(j)$, $\mathbf{R}_+^{n+1} \setminus (U(j) \cup V(j))$ has Lebesgue measure zero.

Next, we need to show that $\mathbf{R}_+^{n+1} \setminus U(1) \cup V(1)$ has Lebesgue measure zero. If $i_k = 1$, then we are done by the prior induction. Assume that $i_k > 1$ and let $j = i_k$. Suppose that $\lim_{t \to \infty} y_i(t) = \hat{y}_i$ for $i \geq i_k$, i.e., $(N(0), P_1(0), \ldots, P_n(0)) \in U(i_k)$. Applying Lemma 4.3 inductively implies that $\lim_{t \to \infty} y_i(t) = \hat{y}_i$ for all $i \geq 1$. Hence, $U(1) = U(i_k)$ and $V(1) = V(i_k)$. Thus, $\mathbf{R}_+^{n+1} \setminus (U(1) \cup V(1))$ has Lebesgue measure zero. Define $U = U(1)$ and $V = V(1)$. If $(N(0), P_1(0), \ldots, P_n(0)) \in U$, then we can argue as in the proof of the second assertion of the theorem that $\liminf_{t \to \infty} N(t) \geq \delta$ for an appropriate choice of $\delta > 0$.

To complete the proof of the final assertion of Theorem 3.2, we need to show that $U(1)$ has positive (possibly infinite) Lebesque measure and that $V(1)$ has infinite Lebesgue measure. The equilibrium $(\hat{y}_1, \ldots, \hat{y}_n)$ for $y_1', \ldots, y_n'$ in (3.1) is linearly stable and its basin of attraction is an open subset of $\mathbf{R}_+^n$. Consequently, $U(1)$ is an open subset of $\mathbf{R}_+^{n+1}$ and has positive Lebesgue measure. To show that $V(1)$ has infinite Lebesgue measure, notice that if $y(0)$ is such that $|y_i(0) - y_i^*|$ is sufficiently small for $i > i_1$ (vacuously true if $i_1 = n$) and $y_{i_1}(0)$ is sufficiently large, then $\lim_{t \to \infty} y_{i_1}(t) = \infty$. Hence, $V(i_1)$ has infinite Lebesgue measure. Since $V(i_1) \subset V(1)$, the proof of the theorem is complete. ☐

5. Weakly search-limited parasitoids. In this section, we examine the effect of including search limitation on the host-parasitoid dynamics.

PROPOSITION 5.1. *Assume* A1–A3. *If* $\lambda > 1$ *and* $a_i > 0$, *then there exists* $\delta > 0$ *such that*

$$\liminf_{t \to \infty} N(t) \geq \delta$$

for all solutions to (2.1) *with* $N(0) > 0$.

Proof. By dissipativity and continuity, system (2.1) has a compact forward invariant set that attracts all nonnegative solutions. Therefore, we can apply the theory of average Lyapunov functions (e.g., see Theorem 2.2 and Corollary 2.3 in [16]) and show that the face $N = 0$ is a repellor. More specifically, the application of the average Lyapunov function $L(N, P_1, \ldots, P_n) = N$ shows that the face $N = 0$ is a repellor since every solution on the face $N = 0$ converges to the origin and $N'/N|_{(N,P_1,\ldots,P_n)=(0,0,\ldots,0)} = \lambda f(0)g_1(0)g_2(0) \cdots g_n(0) = \lambda > 1$. $\square$

Although search-limited parasitoids cannot drive the host extinct, numerical simulations suggest that when purely egg-limited parasitoids can drive their host extinct, the inclusion of search limitation results in the host being suppressed to low equilibrium densities provided that parasitoid attacks are sufficiently aggregated (Figure 5.1b).
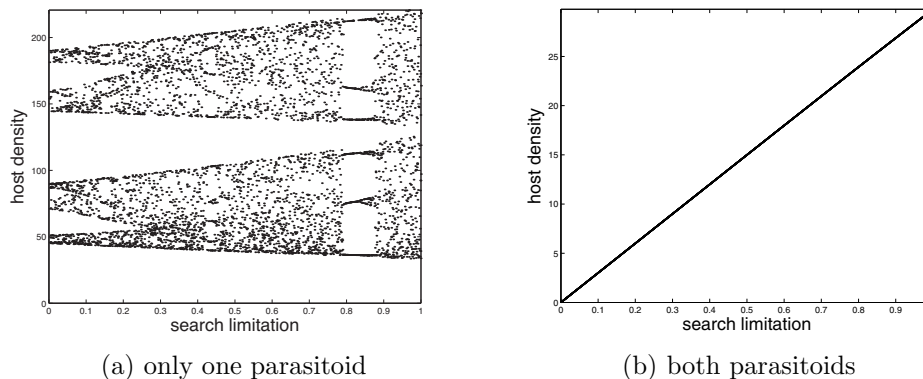

(a) only one parasitoid   (b) both parasitoids

FIG. 5.1. *The effect of single versus multiple parasitoid introductions when parasitoids exhibit search limitation. In* (a), *only one parasitoid is in the system. In* (b), *two parasitoids are in the system. In both figures,* $\lambda = 10$, $k_i = 0.5$, $f(N) = 1/(1 + (0.01N)^4)$, $\theta_i = 2.0$, *and* $b_i = 0.1$. *The parasitoids' searching limitations* $a_1 = a_2$ *vary as shown.*

PROPOSITION 5.2. *Assume* A1–A3. *Let* $(N(t), P_1(t), \ldots, P_n(t))$ *be a solution to* (2.1). *If* $\lambda > 1$ *and* $\theta_m > b_m \lambda$, *and* $a_m > 0$ *is sufficiently small, then there exists* $\delta > 0$ *such that*

$$\liminf_{t \to \infty} P_m(t) \geq \delta$$

whenever $N(0) > 0$ *and* $P_m(0) > 0$. *Alternatively, if* $\theta_i < b_i \lambda$ *for* $m \leq i \leq n$, *then there exists a neighborhood* U *of the* $P_m = P_{m+1} = \cdots = P_n = 0$ *plane such that*

$$\lim_{t \to \infty} (P_m(t) + \cdots + P_n(t)) = 0$$

whenever $(N(0), P_1(0), \ldots, P_n(0))$ *lies in* U. *Moreover, if* $k_i < 1$ *for* $m \leq i \leq n$, *then* $U = \mathbf{R}_+^{n+1}$.

The first statement of Proposition 5.2 shows that if the reproductive ability of the parasitoid is higher than that of the host ($\theta_m/b_m > \lambda$) and there is weak search limitation (small $a_m > 0$), then the parasitoid coexists with its host. This type of coexistence is not always guaranteed if $a_m = 0$. However, if $a_m > 0$ is not small, numerical simulations suggest that the parasitoid may become extinct (see Figure 4 in [28]). The second statement of Proposition 5.2 considers the alternative situation ($\theta_m/b_m < \lambda$). In this case, the parasitoid whose population density is initially low becomes extinct irrespective of the intensity of search limitation. This attractivity result holds globally if the distribution of the parasitoid attack is aggregated ($k_m < 1$). However, this is not true if $k_m > 1$, since the system can have a positive fixed point or attractor. For instance, Figure 5.2 shows an example where a second positive fixed point bifurcates from the origin at $a_1 = 0$. As a_1 increases, this fixed point is stabilized and finally disappears due to a saddle node bifurcation. In this example, we also find a stable invariant loop in advance of the stabilization of the second fixed point (see Figure 5.2). Therefore, intermediate degrees of search limitation can produce a bistable system in which the initially rare parasitoid becomes extinct but the initially abundant parasitoid survives (see Figure 5.3).

Proof. Assume that $\lambda > 1$ and $\theta_m > b_m\lambda$. Proposition 5.1 implies that there is a compact attractor Γ such that the Γ does not intersect the $N = 0$ plane and such that the ω-limit set of $Z(t) = (N(t), P_1(t), \ldots, P_n(t))$ lies in Γ whenever $N(0) > 0$. We will show that Γ intersected with the plane $P_m = 0$ is a repellor whenever $a_m > 0$ is sufficiently small. Let $Z(t) = (N(t), P_1(t), \ldots, P_n(t))$ be a solution to (2.1) with $N(0) > 0$ and $P_m(0) = 0$. Since the ω-limit set of $Z(t)$ lies in Γ, we get that

$$0 = \lim_{t \to \infty} \frac{1}{t} \ln\left(\frac{N(t)}{N(0)}\right)$$

$$= \lim_{t \to \infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln\left(f(N(s))g_1(E_1(s))\ldots g_n(E_n(s))\lambda\right),$$

where $E_i(s) = \frac{P_i(s)}{a_i + b_i N(s)}$. It follows that

$$(5.1) \qquad \lim_{t \to \infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln\left(f(N(s))g_1(E_1(s))\ldots g_n(E_n(s))\right) = -\ln\lambda.$$

Let

$$G_i(N, P_1, \ldots, P_n) = \frac{\partial P_i'}{\partial P_i}.$$

The Lyapunov exponent [24] corresponding to the P_m direction is given by

$$(5.2)$$
$$\liminf_{t \to \infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln G_m(Z(s))$$

$$= \liminf_{t \to \infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln\left(\theta_m N(s) f(N(s)) g_1(E_1(s)) \ldots g_{m-1}(E_i(s)) \frac{1}{a_m + b_m N(s)}\right)$$

$$= \liminf_{t \to \infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln\left(\theta_m N(s) \frac{1}{g_m(E_m(s))} \cdots \frac{1}{g_n(E_n(s))} \frac{1}{a_m + b_m N(s)} \frac{1}{\lambda}\right)$$

$$\geq \liminf_{t \to \infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln\left(\theta_m N(s) \frac{1}{\lambda(a_m + b_m N(s))}\right),$$
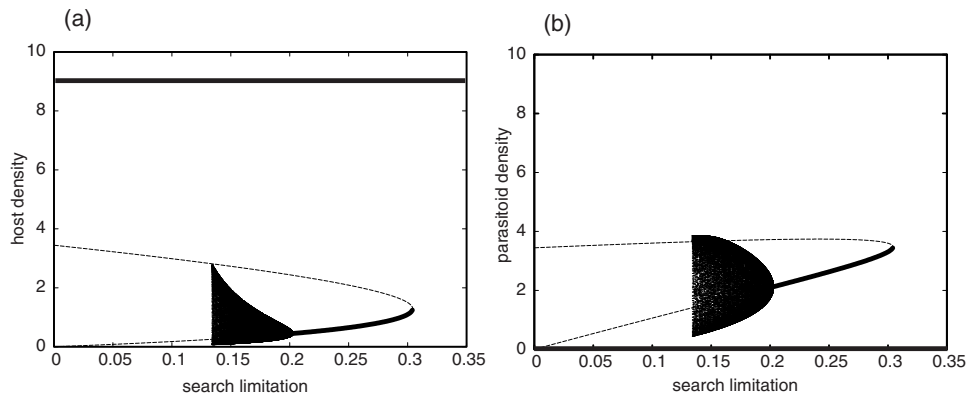
(a)

(b)

FIG. 5.2. *Bifurcation diagram of* (2.1) *with a single parasitoid species* P_1, *i.e.,* $n = 1$. *The solid and dashed curves indicate stable and unstable fixed points, respectively. In both figures,* $f(N) = 1/(1 + N)$, $\lambda = 10$, $b_1 = 1$, $k_1 = 2$, *and* $\theta_1 = 8$. *If there is no search limitation* $(a_1 = 0)$, *the parameters correspond to the conditional extinction case of Theorem* 3.2.
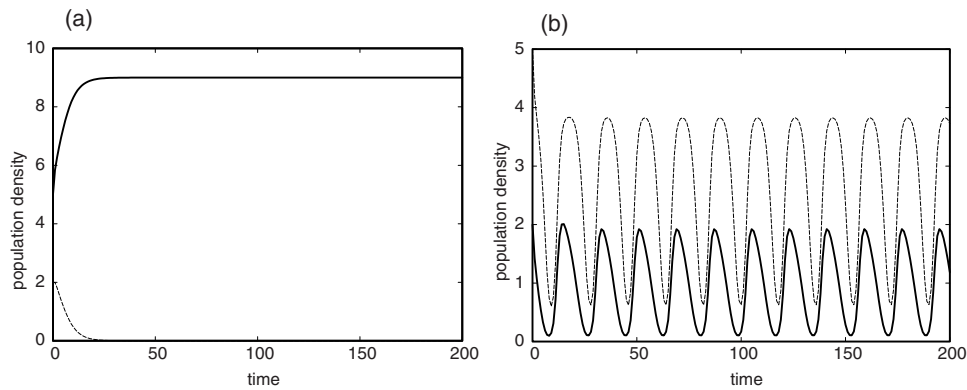
(a)

(b)

FIG. 5.3. *Bistable example of* (2.1) *with a single parasitoid species* P_1, *i.e.,* $n = 1$ *The solid and dashed curves indicate the population density of host and parasitoid, respectively. In both figures, the survival function and parameters are* $f(N) = 1/(1 + N)$, $\lambda = 10$, $a_1 = 0.15$, $b_1 = 1$, $k_1 = 2$, *and* $\theta_1 = 8$. *The initial conditions are* (a) $(N(0), P_1(0)) = (5, 2)$, *and* (b) $(N(0), P_1(0)) = (2, 5)$.

where the second line follows from (5.1) and the third line follows from $1/g_j \geq 1$ for all $1 \leq j \leq n$. If $\theta_m > b_m \lambda$ and $a_m > 0$ is sufficiently small, then (5.2) implies that there exists $\epsilon > 0$ such that

$$(5.3) \qquad \liminf_{t \to \infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln G_m(Z(s)) \geq \epsilon$$

for all initial conditions with $N(0) > 0$ and $P_m(0) = 0$. Equation (5.3) and the average Lyapunov theory (e.g., see Theorem 2.2 in [16]) with the average Lyapunov function $L(N, P_1, \ldots, P_n) = P_m$ implies that Γ intersected with the $P_m = 0$ plane is a repellor. This completes the proof of the first statement.

Assume $\theta_i < b_i \lambda$ for $m \leq i \leq n$ and $a_i \geq 0$ for all i. If $\lambda < 1$, then $\lim_{t \to \infty} P_i(t) = 0$ for all i as $P_i(t+1) \leq \theta_i N(t)$ and we are done. Assume $\lambda > 1$. Proposition 5.1 implies

that there is a compact attractor Γ such that Γ does not intersect the $N = 0$ plane and such that the ω-limit set of $Z(t) = (N(t), P_1(t), \ldots, P_n(t))$ lies in Γ whenever $N(0) > 0$. Let Γ_1 be given by Γ intersected with the $P_m = P_{m+1} = \cdots = P_n = 0$ plane. We will show that Γ_1 is an attractor by proving that all the normal Lyapunov exponents (i.e., the Lyapunov exponents corresponding to Lyapunov directions that are not tangential to the $P_m = P_{m+1} = \cdots = P_n = 0$ plane) are negative (see, e.g., [35, Thm. 4] or [14]). To this end, consider a solution $Z(t) = (N(t), P_1(t), \ldots, P_n(t))$ to (2.1) such that $Z(0) \in \Gamma_1$. Using (5.1) and assuming $m \leq i \leq n$, we get

$$\limsup_{t\to\infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln G_i(Z(s))$$

$$= \limsup_{t\to\infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln \left(\theta_i N(s) \frac{1}{\lambda} \frac{1}{g_i(E_i(s))} \cdots \frac{1}{g_n(E_n(s))} \frac{1}{a_i + b_i N(s)} \right)$$

$$= \limsup_{t\to\infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln \left(\frac{\theta_i}{\lambda} \frac{N(s)}{a_i + b_i N(s)} \right)$$

$$\leq \ln \left(\frac{\theta_i}{\lambda b_i} \right) < 0,$$

where the second line follows from $E_j(s) = 0$ for $m \leq j \leq n$ and the third line follows from $\frac{N}{a_i + b_i N} \leq \frac{1}{b_i}$ whenever $N > 0$. Hence, all the normal Lyapunov exponents are negative and Γ_1 is an attractor. Next, assume that $k_i < 1$ for $m \leq i \leq n$. Let $Z(t)$ be a solution to (2.1) such that $N(0) > 0$. We will prove that

$$\lim_{t\to\infty} P_i(t) = 0 \text{ for } m \leq i \leq n$$

by induction on i. Consider $i = n$. If $P_n(0) = 0$, then we are done. Assume $P_n(0) > 0$. Then

$$\limsup_{t\to\infty} \frac{1}{t} \ln \left(\frac{P_n(t)}{P_n(0)} \right)$$

$$= \limsup_{t\to\infty} \frac{1}{t} \sum_{s=0}^{t-1} \ln \left(\theta_n N(s) f(N(s)) g_1(E_1(s)) \ldots g_{n-1}(E_{n-1}(s)) \frac{(1 - g_n(E_n(s)))}{P_n(s)} \right)$$

$$= \limsup_{t\to\infty} \frac{1}{t} \sum_{s=1}^{t} \ln \left(\theta_n N(s) \frac{1}{\lambda} \left(\frac{1}{g_n(E_n(s))} - 1 \right) \frac{1}{P_n(s)} \right)$$

$$\leq \limsup_{t\to\infty} \frac{1}{t} \sum_{s=1}^{t} \ln \left(\frac{\theta_n}{\lambda} \frac{N(s)}{a_n + b_n N(s)} \right)$$

$$\leq \ln \left(\frac{\theta_n}{\lambda b_n} \right) < 0,$$

where the second line follows from (5.1), the third line follows from $1/g_n(x) - 1$ being concave (i.e., $k_n < 1$), and the fourth line follows from the fact that $\frac{N}{a_n + b_n N} \leq \frac{1}{b_n}$ whenever $N > 0$. Hence, we have shown that $\lim_{t\to\infty} P_n(t) = 0$. Next, we proceed to the inductive step. Assume that $\lim_{t\to\infty} P_i(t) = 0$ for $j + 1 \leq i \leq n$, where $j \geq m$. If

$P_j(0) = 0$, then we are done. Assume $P_j(0) > 0$. Then

$$\limsup_{t\to\infty} \frac{1}{t}\ln\left(\frac{P_j(t)}{P_j(0)}\right)$$

$$= \limsup_{t\to\infty} \frac{1}{t}\sum_{s=0}^{t-1}\ln\left(\theta_j N(s)f(N(s))g_1(E_1(s))\dots g_{j-1}(E_{j-1}(s))\frac{(1-g_j(E_j(s)))}{P_j(s)}\right)$$

$$= \limsup_{t\to\infty} \frac{1}{t}\sum_{s=0}^{t-1}\ln\left(\theta_j N(s)\frac{1}{\lambda}\frac{1}{g_{j+1}(E_{j+1}(s))}\dots\frac{1}{g_n(E_n(s))}\left(\frac{1}{g_j(E_j(s))}-1\right)\frac{1}{P_j(s)}\right)$$

$$= \limsup_{t\to\infty} \frac{1}{t}\sum_{s=0}^{t-1}\ln\left(\theta_j N(s)\frac{1}{\lambda}\left(\frac{1}{g_j(E_j(s))}-1\right)\frac{1}{P_j(s)}\right)$$

$$\le \limsup_{t\to\infty} \frac{1}{t}\sum_{s=0}^{t-1}\ln\left(\frac{\theta_j}{\lambda}\frac{N(s)}{a_j+b_j N(s)}\right)$$

$$\le \ln\left(\frac{\theta_j}{\lambda b_j}\right) < 0,$$

where the second line follows (5.1), the third line follows from induction (i.e., $g_i(0) = 1$ for $j < i \le n$), the fourth line follows from $1/g_j(x) - 1$ being concave (i.e., $k_j < 1$), and the final line follows from the fact that $\frac{N}{a_j+b_j N} \le \frac{1}{b_j}$ whenever $N > 0$. Hence, we have shown that $\lim_{t\to\infty} P_j(t) = 0$, and the proof is complete. $\qquad\square$

6. Discussion. We have studied the multiparasitoid-host dynamics described by (2.1). Under the assumption that each parasitoid is purely egg limited (i.e., not search limited), the dynamics of (2.1) have been classified sharply with respect to the extinction and persistence dynamics (see Theorem 3.2). Our main result implies that for the systems considered here, multiple parasitoids regulate a host population more efficiently than a single parasitoid. This conclusion can be derived for the following three scenarios in which the parasitoids can regulate the host:

(i) There are parasitoids with aggregated attacks ($k_i < 1$ for all i) such that $\lambda g_1(y_1^*)\cdots g_n(y_n^*) < 1$. This assembly of parasitoids drives the host extinct. The definition of y_i^* and concavity of $1/g_i$ (as $k_i < 1$) imply that y_i^* is greater when you include more parasitoid species. Since $g_i(y_i^*) < 1$ and g_i is a decreasing function for all i, the inequality $\lambda g_1(y_1^*)\cdots g_n(y_n^*) < 1$ is more likely to hold if there are multiple aggregately distributed parasitoids irrespective of their superiority within a parasitized host (see Figures 3.1 and 3.2(a),(b)).

(ii) There are parasitoids with aggregated attacks ($k_i < 1$ for all i) such that $\lambda g_1(\hat{y}_1)\cdots g_n(\hat{y}_n) > 1$. This assembly of parasitoids does not drive the host extinct. Rather, they coexist with the host. As mentioned in section 3 (see also Corollary 3.3), after the establishment of these parasitoids, the dynamics of the host are asymptotic to

$$N' = \lambda f(N)N\prod_{i=1}^{n}g_i(y_i^*).$$

This equation suggests that introductions of multiple parasitoids lead to more efficient regulation of the host population. In fact, the last factor of the equation depresses the host density at a coexistence equilibrium.

(iii) There exists a highly reproductive parasitoid ($y_i^* = 0$) whose attacks are weakly aggregated ($k_i > 1$). By the definition of y_i^*, $y_i^* = 0$ if

$$\theta_i > b_i \lambda g_{i+1}(\hat{y}_{i+1}) \cdots g_n(\hat{y}_n).$$

This inequality is more likely to hold if there are multiple aggregately distributed parasitoids that are superior competitors within the parasitized host (i.e., P_j with $k_j < 1$, $j > i$).

The conclusion that multiple parasitoid introductions are more effective than single parasitoid introductions could depend on model assumptions. The main assumptions in our model are that the parasitoids are egg limited; the host suffers density-dependent mortality between the events of parasitism and death due to the parasitism; and the distributions of attacks of parasitoids are independent of each other. Kakehashi, Suzuki, and Iwasa [18] found that introductions disrupted host regulation when the distributions of parasitoid attacks completely overlap. Therefore, we expect that incorporation of overlapping parasitoid distributions into our model may lead to a similar conclusion. Interestingly, our conclusion seems insensitive to other assumptions. For example, our conclusion agrees with that of May and Hassell [21], who assume purely search-limited parasitism and no host density dependence.

REFERENCES

[1] M. BENAÏM AND M. W. HIRSCH, *Asymptotic pseudotrajectories and chain recurrent flows, with applications*, J. Dynam. Differential Equations, 8 (1996), pp. 141–176.

[2] C. J. BRIGGS, *Competition among parasitoid species on a stage-structured host and its effect on host suppression*, The American Naturalist, 141 (1993), pp. 372–397.

[3] F. J. CHOW AND M. MACKAUER, *Inter- and intraspecific larval competition in aphidius smithi and praon pequodorum (hymenoptera: aphidiidae)*, Canadian Entomologist, 116 (1984), pp. 1097–1107.

[4] P. DEBACH, *Biological Control of Insect Pests and Weeds*, W. H. Rheinhold, New York, 1964.

[5] L. E. EHLER AND R. W. HALL, *Evidence for competitive exclusion of introduced natural enemies in biological control*, Environmental Entomology, 11 (1982), pp. 1–4.

[6] W. M. GETZ AND N. J. MILLS, *Host-parasitoid coexistence and egg-limited encounter rates*, The American Naturalist, 148 (1996), pp. 333–347.

[7] H. C. J. GODFRAY, *Parasitoids*, Princeton University Press, Princeton, NJ, 1994.

[8] D. J. GREATHEAD AND A. H. GREATHEAD, *Biological control of insect pests by insect parasitoids and predators: The biocat database*, Biocontrol News Info., 13 (1992), pp. 61N–68N.

[9] M. P. HASSELL, *The Dynamics of Arthropod Predator-Prey Systems*, Monographs in Population Biology 13, Princeton University Press, Princeton, NJ, 1978.

[10] M. P. HASSELL AND R. M. MAY, *Stability in insect host-parasite models*, Journal of Animal Ecology, 42 (1973), pp. 693–726.

[11] M. P. HASSELL, R. M. MAY, S. W. PACALA, AND P. L. CHESSON, *The persistence of host-parasitoid associations in patchy environments. I. A general criterion*, The American Naturalist, 138 (1991), pp. 586–583.

[12] G. E. HEIMPEL AND J. A. ROSENHEIM, *Egg limitation in parasitoids: A review of the evidence and a case study*, Biological Control, 11 (1998), pp. 160–168.

[13] M. E. HOCHBERG AND R. D. HOLT, *Refuge evolution and the population dynamics of coupled host-parasitoid associations*, Evolutionary Ecology, 9 (1995), pp. 633–661.

[14] J. HOFBAUER AND S. J. SCHREIBER, *To persist or not to persist?*, Nonlinearity, 17 (2004), pp. 1393–1406.

[15] C. B. HUFFAKER, *Biological Control*, Plenum, New York, 1971.

[16] V. HUTSON, *A theorem on average Liapunov functions*, Monatsh. Math., 98 (1984), pp. 267–275.

[17] M. A. JERVIS, G. E. HEIMPEL, P. N. FERNS, J. A. HARVEY, AND N. A. C. KIDD, *Life-history strategies in parasitoid wasps: A comparative analysis of 'ovigeny'*, Journal of Animal Ecology, 70 (2001), pp. 442–458.

[18] M. Kakehashi, Y. Suzuki, and Y. Iwasa, *Niche overlap of parasitoids in host-parasitoid systems: Its consequences to single versus multiple introduction controversy in biological control*, Journal of Applied Ecology, 21 (1984), pp. 115–131.

[19] S. D. Lane, N. J. Mills, and W. M. Getz, *The effects of parasitoid fecundity and host taxon on the biological control of insect pests: The relationship between theory and data*, Ecological Entomology, 24 (1999), pp. 181–190.

[20] R. M. May, *Host-parasitoid systems in patch environments: A phenomenological model*, Journal of Animal Ecology, 47 (1978), pp. 833–843.

[21] R. M. May and M. P. Hassell, *The dynamics of multiparasitoid-host interactions*, The American Naturalist, 117 (1981), pp. 234–261.

[22] R. M. May, M. P. Hassell, R. M. Anderson, and D. W. Tonkyn, *Density dependence in host-parasitoid models*, Journal of Animal Ecology, 50 (1981), pp. 855–865.

[23] N. J. Mills and W. M. Getz, *Modelling the biological control of insect pests: A review of host-parasitoid models*, Ecol. Model., 92 (1996), pp. 121–143.

[24] V. I. Oseledec, *A multiplicative ergodic theorem*, Trans. Moscow Math. Soc., 19 (1968), pp. 197–231.

[25] C. Robinson, *Stability theorems and hyperbolicity in dynamical systems*, Rocky Mountain J. Math., 7 (1977), pp. 425–437.

[26] D. J. Rogers, *Random search and insect population models*, Journal of Animal Ecology, 41 (1972), pp. 369–383.

[27] S. J. Schreiber, *Host-parasitoid dynamics of a generalized Thompson model*, J. Math. Biol., 52 (2006), pp. 719–732.

[28] S. J. Schreiber, *Periodicity, persistence, and collapse in host-parasitoid systems with egg limitation*, J. Biol. Dyn., 1 (2007), pp. 273–288.

[29] S. J. Schreiber, N. J. Mills, and A. P. Gutierrez, *Host-limited dynamics of autoparasitoids*, J. Theoret. Biol., 212 (2001), pp. 141–153.

[30] K. Shea, R. M. Nisbet, W. W. Murdoch, and H. J. S. Yoo, *The effect of egg limitation on stability in insect host-parasitoid population models*, Journal of Animal Ecology, 65 (1996), pp. 743–755.

[31] W. R. Thompson, *La theory mathematique de l'action des parasites entomophages et le facteur du hassard*, Ann. Fac. Sci. Marseille, 2 (1924), pp. 69–89.

[32] A. L. Turnbull and D. A. Chant, *The practice and theory of biological control of insects in Canada*, Canadian Journal of Zoology, 39 (1961), pp. 697–753.

[33] R. Van den Bosch, *Comments on population dynamics of exotic insects*, Bulletin of the Entomological Society of America, 14 (1968), pp. 112–115.

[34] K. E. F Watt, *Community stability and the strategy of biological control*, Canadian Entomologist, 97 (1965), pp. 887–895.

[35] L. Xu, B. Chen, Y. Zhao, and Y. Cao, *Normal Lyapunov exponents and asymptotically stable attractors*, Dyn. Syst., 23 (2008), pp. 207–218.