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Periodicity, persistence, and collapse in host–parasitoid systems with egg limitation

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There is an emerging consensus that parasitoids are limited by the number of eggs which they can lay as well as the amount of time they can search for their hosts. Since egg limitation tends to destabilize host–parasitoid dynamics, successful control of insect pests by parasitoids requires additional stabilizing mechanisms such as heterogeneity in the distribution of parasitoid attacks and host density-dependence. To better understand how egg limitation, search limitation, heterogeneity in parasitoid attacks, and host density-dependence influence host–parasitoid dynamics, discrete time models accounting for these factors are analyzed. When parasitoids are purely egg-limited, a complete anaylsis of the host–parasitoid dynamics are possible. The analysis implies that the parasitoid can invade the host system only if the parasitoid's intrinsic fitness exceeds the host's intrinsic fitness. When the parasitoid can invade, there is a critical threshold, $CV^* > 1$, of the coefficient of variation (CV) of the distribution of parasitoid attacks that determines that outcome of the invasion. If parasitoid attacks sufficiently aggregated (i.e., $CV > CV^*$), then the host and parasitoid coexist. Typically (in a topological sense), this coexistence is shown to occur about a periodic attractor or a stable equilibrium. If the parasitoid attacks are sufficiently random (i.e. $CV < CV^*$), then the parasitoid drives the host to extinction. When parasitoids are weakly search-limited as well as egg-limited, coexistence about a global attractor occurs even if $CV < CV^*$. However, numerical simulations suggest that the nature of this attractor depends critically on whether $CV < 1$ or $CV > 1$. When $CV < 1$, the parasitoid exhibits highly oscillatory dynamics. Alternatively, when parasitoid attacks are sufficiently aggregated but not overly aggregated (i.e. $CV > 1$ but close to 1), the host and parasitoid coexist about a stable equilibrium with low host densities. The implications of these results for classical biological control are discussed.

Keywords: Egg limitation; Search limitation; Host–parasitoid interactions; Biological control; Spatial heterogeneity; Permanence

1. Introduction

Parasitoids are organisms, typically wasps and flies, whose young develop on and eventually kill their hosts. Despite their diminutives size, parasitoids are an incredibly successful life-form that account for 10% or more of metazoan species. Moreover, parasitoids have been extremely successful in suppressing the abundance of insect pests. To better understand the basis for their success, models of host–parasitoid interactions have been studied extensively.

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Traditionally, these models have assumed that the parasitoids are limited primarily by their ability to locate hosts [1–8]. This assumption, however, neglects the fact that parasitoids may be limited by the number of eggs available for oviposition. In the past decade, there has been an emerging consensus that parasitoids can be limited by egg supply as well as time available for locating hosts [9–13]. Reflecting this consensus, several theoretical studies have examined the combined effects of egg limitation and search limitation on host–parasitoid dynamics [9, 13–15]. While providing key insights, these studies assumed that the hosts exhibit exponential growth in the absence of the parasitoids. Moreover, they focused on equilibrium stability. Since all host populations experience some level of intraspecific density-dependence and host–parasitoid populations may exhibit oscillatory behavior, I analyze the global dynamics of a general class of host–parasitoid models that account for search limitation, egg limitation, and host density-dependence.

All parasitoids experience egg limitation to some degree [9–12]. This egg limitation comes in a variety of forms. Synovigenic parasitoids which continuously produce egg over their lifetime experience egg limitation whenever the number of hosts encounter in a day exceeds their daily production of eggs. For instance, in a study, Heimpel and Rosenheim [10] 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. At the other end of the spectrum, pro-ovigenic parasitoids which are born with a fixed complement of eggs experience egg limitation whenever the number of hosts they encounter in their lifetime exceeds their complement of eggs. Pro-ovigenic species appear to be rare. Javis *et al.* [11] found that only 12 out of 683 parasitoid species are pro-ovigenic. The remaining 626 species were classified as synovigenic. However, amongst these synovigenic species, there was considerable variability in the fraction of mature eggs that were produced after their emergence from the host. Hence, most species lie between the extremes of emerging with a complete complement of mature eggs and emerging with no mature eggs.

Since hosts and parasitoids tend to have synchronized generations in seasonal environments, their dynamics are often modeled with difference equations [3, 16]. An important component of these difference equation is the host encounter rate E, which describes the average number of attacks or parasitic encounters per host. Based on the foundational work of Nicholson and Bailey [17], studies of host–parasitoid models traditionally assume that the encounter rate only depends on the density of the parasitoid [1–8, 18]. This assumption, however, neglects the fact that at higher host densities, parasitoids are more likely to be egg-limited and, consequently, less likely to attack hosts. If one takes a broad view that egg limitation is a form of predator saturation, then Rogers [15] 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 [14] 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 [9] 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. In contrast, May [4] found in models without egg limitation that stability only requires parasitic attacks to be sufficiently aggregated. Getz and Mills [9, p. 341] concluded 'our analysis leads us to question whether the assumption that parasitoid encounter rates are determined purely by limitations in searching efficiency . . . should underpin more elaborate discrete time host–parasitoid models that include, for example, interference competition or host self-regulation.'

Since host dynamics are typically self-regulated and this self-regulation can be stabilizing, I develop and analyze a discrete time model of host–parasitoid interactions that accounts for search limitation, egg limitation, heterogeneity in the distribution of parasitoid attacks, and host density-dependence. The model is presented in section 2. In section 3, I analyze the model when the parasitoids are egg-limited but not search-limited. The rationale for looking at this extreme is twofold. First and foremost, an analysis of this case allows one to see how egg limitation, in and of itself, influences host–parasitoid dynamics and thereby provides a natural counterpart to pre-existing theory which assume parasitoids are purely search-limited. Second, these models are analytically quite tractable and, consequently, their global dynamics can be much better understood than other host–parasitoid models. In section 4, I investigate the combined effects of search limitation and egg limitation. In particular, a characterization of global coexistence is proven. The proofs of all the results are relegated to the Appendix. Section 5 discusses the implications of these results for classical biological control.

2. The model

The discrete time model describes the dynamics of host–parasitoid populations with synchronized generations. The host of density H is subject to parasitism by a parasitoid of density P. The fraction $g(E)$ of hosts escaping parasitism depends on the host encounter rate E, 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. [5, 19, 20]). 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. Parasitized hosts that escape density-dependent mortality produce on average θ parasitoids that survive to the next generation. Under these assumptions, the model is given by

$$\begin{aligned} N' &= \lambda N f(N) g(E) \\ P' &= \theta N f(N)(1 - g(E)), \end{aligned} \tag{1}$$

where N' and P' are the densities of the host and parasitoid, respectively, in the next generation. The state space for the host–parasitoid dynamics is $\mathbf{R}^2_+ = \{(N, P) \in \mathbf{R}^2 : N \geq 0, P \geq 0\}$.

To complete the model, it is necessary to specify the density-dependent survivorship function $f(N)$, the encounter rate function E, and the escape function g. Throughout this article, I assume that

A1: f is a continuously differentiable, 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 $f(N) = 1/(1 + \alpha N^{\beta})$ with $\alpha > 0$ and $\beta > 0$, the Ricker functions $f(N) = \exp(-\alpha N)$ with $\alpha > 0$, and the Hassell function $f(N) = 1/(1 + \alpha N)^{\beta}$. To account simultaneously for search limitation and egg limitation, I follow the approach of Rogers [15] and define the average host encounter rate as

$$E = \frac{\alpha P}{1 + \alpha b N},$$

where α is the searching efficiency of the parasitoid and b corresponds to the handling time or egg limitation of the parasitoid. For parsimony, I rewrite this average encounter rate as

$$E = \frac{P}{a + bN}, \tag{2}$$

where $a = 1/\alpha$. One can view a as a measurement of search limitation. When there is no egg limitation (i.e. $b = 0$), the encounter rate reduces to the classical Nicholson–Bailey search-limited encounter rate of $E = P/a$. Alternatively, when there is no search limitation (i.e. $a = 0$), the encounter rate reduces to the Thompson model $E = P/(bN)$ of egg-limited encounter rates [20, 21]. If eggs are randomly laid on hosts, then the fraction of hosts, then the fraction of hosts escaping parasitism is $\exp(-E)$. More generally, the Poisson escape term $\exp(-E)$ can be viewed as a limiting case of the negative binomial escape term $(1 + E/k)^{-k}$ as $k \uparrow \infty$. This negative binomial escape function is commonly used to model non-random or aggregated parasitism events [3, 4, 9, 19]. In particular, $1/k$ can be interpreted as the coefficient of variation squared (CV^2) of the host encounter rate [22]. Consequently, larger values of k correspond to parasitic attacks being more evenly distributed across the hosts, while smaller values of k correspond to parasitoid attacks being aggregated on fewer hosts. To allow for this continuum of possibilities, I assume throughout this article that

A2: $g(E) = (1 + E/k)^{-k}$ and $E = P/(a + bN)$ with $k > 0$ (possibly ∞), $a \geq 0$, and $b \geq 0$.

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

3. Egg-limited dynamics

When the parasitoids are egg-limited but not search-limited (i.e. $a = 0$ and $b > 0$), the model can be analyzed rather completely. The key to this analysis is the change of variables $y_1 = N$ and $y_2 = P/N$. With respect to this change of variables, equation (1) with $a = 0$, $b > 0$ partially decouples

$$\begin{aligned} y_1' &= \lambda y_1 f(y_1) g(y_2) \\ y_2' &= \frac{\theta}{\lambda}((1 + y_2/(bk))^k - 1), \end{aligned} \tag{3}$$

where y_i' is the value of y_i in the next generation. An important quantity associated with these equations is

$$y_2^* = \max\left\{ y_2 : \frac{\theta}{\lambda}((1 + y_2/(bk))^k - 1) = y_2 \right\}$$

which exists whenever $k \neq 1$. The quantity y_2^* corresponds to the largest equilibrium ratio of parasitoids to hosts. Using this change of variables, I previously proved the following theorem [20].

THEOREM 3.1 *Assume $a = 0$ and $b > 0$. Then equation (1) exhibits the following dynamics*:
Host failure: *If $\lambda < 1$, then*

$$\lim_{n \to \infty} (N_n, P_n) = (0, 0)$$

whenever $N_0 \geq 0$ and $R \geq 0$.
Parasitoid failure: *If $\lambda > 1$, $k < 1$, and $\theta/b < \lambda$, then there exist $M > m > 0$ such that*

$$\lim_{n \to \infty} P_n = 0 \quad \textit{and} \quad M \geq N_n \geq m \quad \textit{for} \quad n \quad \textit{sufficiently large}$$

whenever $N_0 > 0$ and $P_0 > 0$.

Coexistence: *If* $\lambda g(y_2^*) > 1$, $\theta/b > \lambda$ *and* $k < 1$, *then there exist* $M > m > 0$ *such that*

$$M \geq N_n \geq m \quad M \geq P_n \geq m$$

whenever $N_0 > 0$, $P_0 > 0$, *and n is sufficiently large.*

Unconditional parasitoid-driven extinction: *If* $k > 1$, $\theta/b > \lambda > 1$ *or* $k < 1$, $\lambda g(y_2^*) < 1 < \lambda$, *then*

$$\lim_{n\to\infty} (N_n, P_n) = (0, 0)$$

whenever $N_0 > 0$ *and* $P_0 > 0$.

Conditional parasitoid-driven extinction: *If* $k > 1$ *and* θ/b, *then there exist* $M > m > 0$ *such that*

$$\lim_{n\to\infty} (N_n, P_n) = (0, 0)$$

whenever $P_0/N_0 > y_2^*$ *and*

$$\lim_{n\to\infty} P_n = 0 \quad \textit{and} \quad M \geq N_n \geq m \quad \textit{for} \quad n \quad \textit{sufficiently large}$$

whenever $0 < P_0/N_0 < y_2^*$.

Theorem 3.1 implies that parasitoid can invade the host system only if its intrinsic fitness θ/b exceeds the intrinsic fitness λ of the host. This invasion can result in coexistence or over-exploitation of the host. Which outcome occurs when is discussed further in the next subsection. When there is more information about the density-dependent survivorship function $f(N)$, it is possible to provide much stronger results about the dynamical nature of this coexistence. For instance, if density-dependent survivorship of the host is given by the Beverton–Holt function $f(N) = 1/(1 + \alpha N)$ with $\alpha > 0$, then coexistence implies convergence to a globally stable equilibrium: $N^* = (\lambda g(y_2^*) - 1)/\alpha$ and $P^* = y_2^* N^*$. In general, however, the dynamics of the host can be quite complex, e.g. exhibit periodic and chaotic dynamics. Since the host–parasitoid dynamics with $a = 0$ are asymptotic to the host's dynamics, the host–parasitoid dynamics can be equally complicated. Despite the possibility of chaotic attractors, the following result is proved in the Appendix. To state this result, given a point $x \in \mathbf{R}_+^2$ and a finite set $\mathcal{O} \subset \mathbf{R}_+^2$ define $\mathrm{dist}(x, \mathcal{O}) = \max_{y\in\mathcal{O}} |x - y|$ to be the distance between the point and the set.

THEOREM 3.2 *Assume that* $k < 1$ *and* $f(N) = \exp(-\alpha N)$ *is the Ricker survivorship function with* $\alpha > 0$. *Then there exists an open and dense set of parameters* (λ, θ, b) *for which there exists a periodic orbit* $\mathcal{O}$ *(possibly of period 1) such that solutions to* (1) *satisfy*

$$\lim_{n\to\infty} \mathrm{dist}((N_n, P_n), \mathcal{O}) = 0$$

for an open set of initial conditions (N_0, P_0) *with full Lebesgue measure.*

Theorem 3.2 implies that for 'most' parameters (in a topological sense) and 'most' initial conditions (in a topological and measure theoretic sense), the host parasitoid dynamics converge either to an equilibrium or a periodic motion. Similar results can be proven for the Hassell and generalized Beverton–Holt survivorship functions. The proof of this result 'lifts' recent results of Kozlovski [23] for one-dimensional dynamics to the dynamics of equation (1). Despite the fact that 'most' parameters in a topological sense have simple 'observable' dynamics, maps such as the Ricker map can exhibit more complicated observable dynamics for parameter values that form a set of positive Lebesgue measure [24]. More specifically, for these parameters, the Ricker map supports an absolutely continuous measure that provides a statistical description of the dynamics for almost every initial condition. It would be interesting to know whether or not this result for one-dimensional dynamics can be ‘lifted’ to the multidimensional host–parasitoid dynamics.

3.1 *Coexistence and collapse*

By studying the way parameters affect the equilibrium y_2^*, one can use Theorem 3.1 to understand how parameters influence species coexistence and parasitoid-driven extinction. Here, I consider the effects of the egg limitation and the aggregation of parasitoid attacks on host–parasitoid dynamics. To keep things focused, I assume throughout this section that the density-dependent survivorship term is of the Ricker form $f(N) = \exp(-N)$ and the host intrinsic fitness λ is greater than one.

Consider the effect of the aggregation parameter k on the dynamics. To allow for coexistence, assume that the intrinsic fitness θ/b of the parasitoid exceeds the host's intrinsic fitness λ. A straightforward calculation reveals that the equilibrium ratio y_2^* of parasitoids to hosts increases without bound as k increases from zero to one. Hence, parasitoids whose attacks are sufficiently aggregated (i.e. $k < \overline{k}$ where $\overline{k} < 1$ is such that $\lambda g(y_2^*) =$) coexist with the host. Moreover, as the equilibrium ratio y_2^{ast} of parasitoids to hosts increases with k, the fraction of hosts escaping parasitism decreases with k. This decrease in the fraction of hosts escaping parasitism tends to stabilize the host–parasitoid dynamics until the aggregation parameter reaches the threshold value of $\overline{k}$. Beyond this threshold, parasitoid attacks are distributed sufficiently randomly to drive the host to extinction. The effects of the aggregation parameter on the host–parasitoid dynamics are illustrated in figure 1.

Next, consider the effect of the egg limitation on the host–parasitoid dynamics. If the parasitoid attacks are sufficiently aggregated (i.e. $k < 1$), then it can be shown that the equilibrium ratio y_2^* of parasitoids to hosts decreases with the egg limitation parameter b. Moreover, y_2^* equals zero whenever egg limitation is sufficiently strong (i.e. $b > \theta/\lambda$). Consequently, when parasitoid egg limitation is sufficiently strong, the host persists and the parasitoid is unable to invade. Alternatively, if the parasitoid egg limitation is too weak (i.e. $b < \overline{b}$ where $\overline{b}$ is such that $\lambda g(y_2^*) = 1$), then the parasitoid drives the host to extinction. Only at intermediate levels of egg limitation (i.e. $\lambda/\theta > b > \overline{b}$) are the host and parasitoid able to coexist. This phenomena of persistence at intermediate parasitic egg loads is illustrated in figure 2.

4. Including search limitation

A detailed understanding of the host–parasitoid dynamics with search limitation and egg limitation provides significant mathematical challenges. However, I am able to provide a criterion for permanence in which the species are able to coexist about a global attractor bounded away from extinction. Permanence ensures that the species persist following large yet rate perturbations [25]. To state this criterion, for a sequence x_n of positive numbers, define the geometric mean of x_n

$$\langle x_n \rangle_G = \lim_{n\to\infty} \left(\prod_{i=1}^{n} x_n \right)^{1/n}$$

whenever the limit is well-defined.

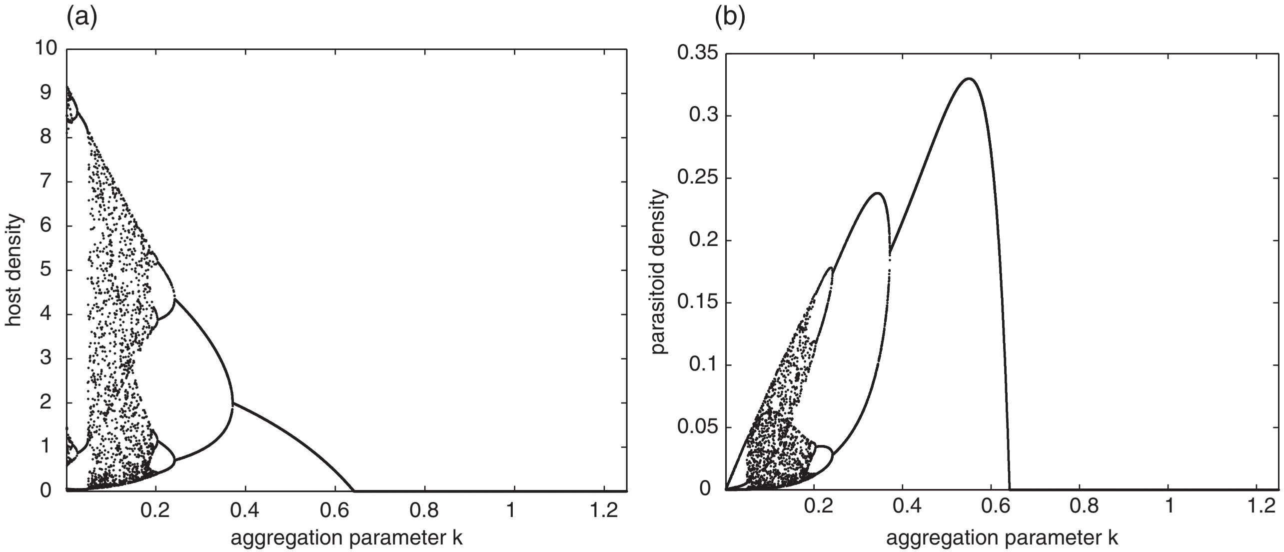

Figure 1. Effect of aggregated attacks on host–parasitoid dynamics without search limitation. In both figures, $f(N) = \exp(-N)$, $\lambda = 25$, $a = 0$, $b = 0.01$, and $\theta = 1$.

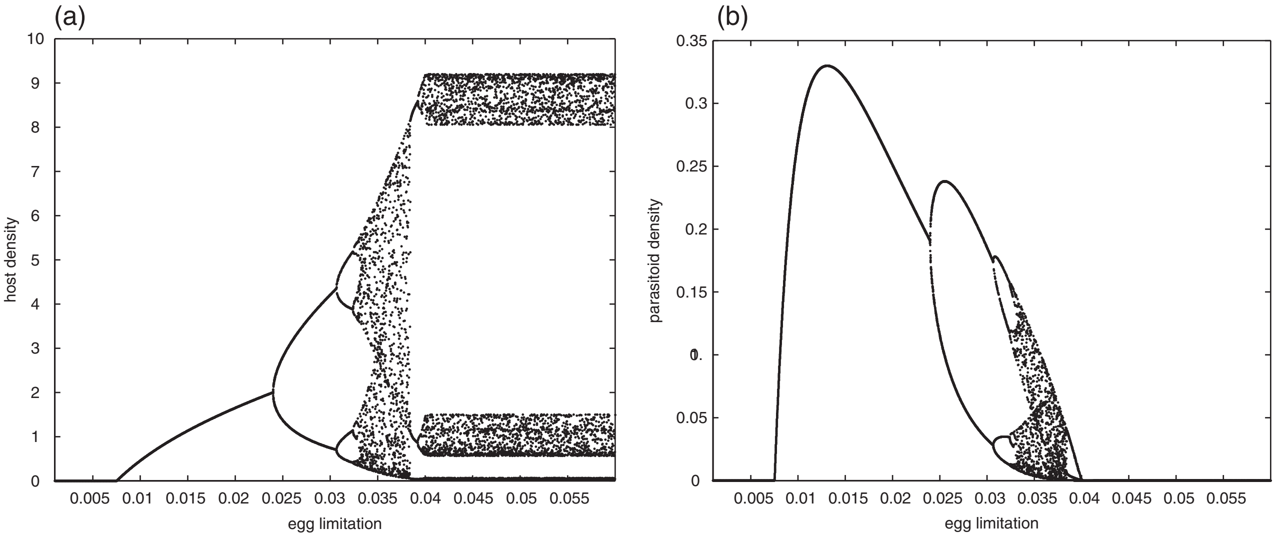

Figure 2. Effects of egg limitation on host–parasitoid dynamics without search limitation. In both figures, $f(N) = \exp(-N)$, $\lambda = 25$, $a = 0$, $k = 0.8$ and $\theta = 1.5$.

THEOREM 4.1 *Let* $a > 0$ *and* $\lambda > 1$. *If*

$$\left\langle \frac{\theta N_n}{a + bN_n} \right\rangle_G > \lambda \tag{4}$$

for any positive solution to the host dynamics $N' = \lambda N f(N)$ *for which* $\langle(\theta N_n)/(a + bN_n)\rangle_G$ *is defined, then equation* (1) *is permanent. Alternatively, if* f *and* $g(E)$ *are twice continuously differentiable and there is a positive solution* N_n *to* $N' = \lambda N f(N)$ *such that*

$$\left\langle \frac{\theta N_n}{a + bN_n} \right\rangle_G < \lambda$$

then (1) *is not permanent.*

Equation (4) has a simple interpretation. The host encounter rate function $E = P/(a + bN)$ is based on the type II functional response $N/(a + bN)$ of the parasitoid. Since θ is the number of parasitoids emerging from a parasitized host, $\theta N/(a + bN)$ can be interpreted as the numerical response of the parasitoid. In fact, this interpretation becomes precise when the parasitoids are at arbitrarily low densities. Hence, equation (4) states that if the geometric mean of the parasitoid's numerical response exceeds the intrinsic fitness of the host, then the host and parasitoid coexist about a global attractor bounded away from extinction. Conversely, if the geometric mean of the parasitoid's numerical response is less than the intrinsic fitness of the host, then there are positive population trajectories that lead to the extinction of the parasitoid.

If the host exhibits simple dynamics, then it is possible to evaluate equation (4) explicitly. For instance, if host density-dependence is modeled with the Beverton–Holt function $f(N) = 1/(1 + \alpha N)$, then it suffices to verify equation (4) at the host equilibrium $N^* = \lambda - 1/\alpha$. In which case, coexistence about a global attractor occurs if $\theta(\lambda - 1)/(a\alpha + b(\lambda - 1)) > \lambda$. When the host exhibits more complicated dynamics (e.g. periodic orbits of high period or chaotic orbits), equation (4) is generally difficult to evaluate explicitly. However, if search limitation is sufficiently weak (as one might expect for a good bio-control agent), then an explicit criterion can be derived. For $\lambda > 1$, it is not hard to prove that

$$\lim_{a \to 0^+} \left\langle \frac{\theta N_n}{a + bN_n} \right\rangle_G = \theta/b$$

for any positive solition N_n to $N' = \lambda N f(N)$ for which the geometric means are defined. Therefore, if the parasitoid's intrinsic fitness exceeds the host's intrinsic fitness (i.e. $\theta/b > \lambda$) and the parasitoid search limitation is sufficiently weak (i.e. $a > 0$ is sufficiently small), then the host and parasitoid coexist about a global attractor. Interestingly, this assertion does not apply in the complete absence of search limitation. Indeed, Theorem 3.1 implies that when $a = 0$, coexistence additionally requires that parasitoid attacks are sufficiently aggregated (i.e. $k < 1$) and $\lambda g(y^*) > 1$. The mathematical reason for this discrepancy between the absence of search limitation and weak search limitations lies in the fact that the equations for the host–parasitoid dynamics are not differentiable at the origin when $a = 0$. The ecological interpretation of this discrepancy is simple. When parasitoids are not search-limited, they are able to track down every last host even when host densities are arbitrarily low. In which case, the parasitoids drive the hosts and themselves to deterministic extinction. However, when the parasitoids have the slightest amount of search limitation, the hosts are able to escape parasitism at low densities and the populations persist.

Comparing figure 1 with figure 3 illustrates how weak search limitation alter the dynamics of host–parasitoid interactions with egg limitation. In particular, these figures show that for sufficiently randomly distributed attacks of the parasitoid (i.e. $k > 0.65$), weak search limitation

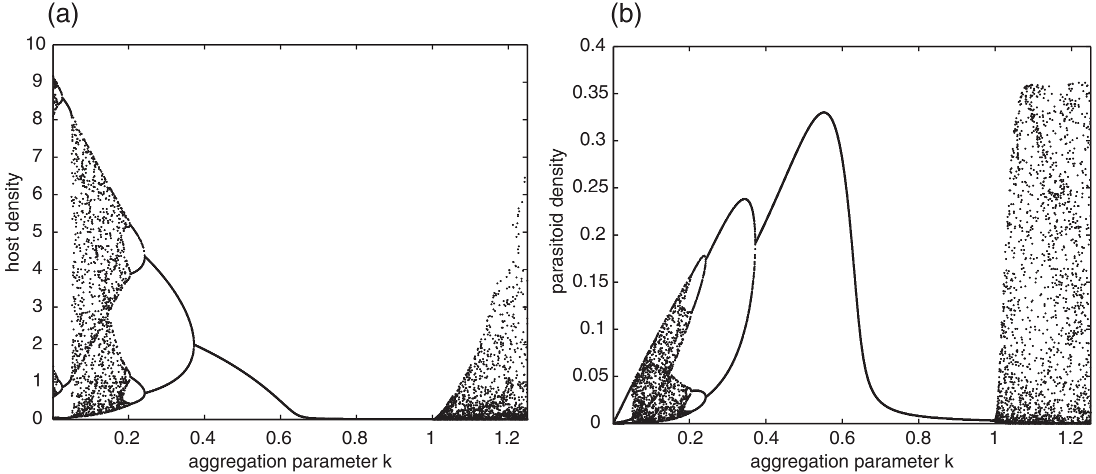

Figure 3. Effect of weak search limitation and aggregated attacks on host–parasitoid dynamics. In both figures, $f(N) = \exp(-N)$, $\lambda = 25$, $a = 0.0001$, $b = 0.01$, and $\theta = 1$.

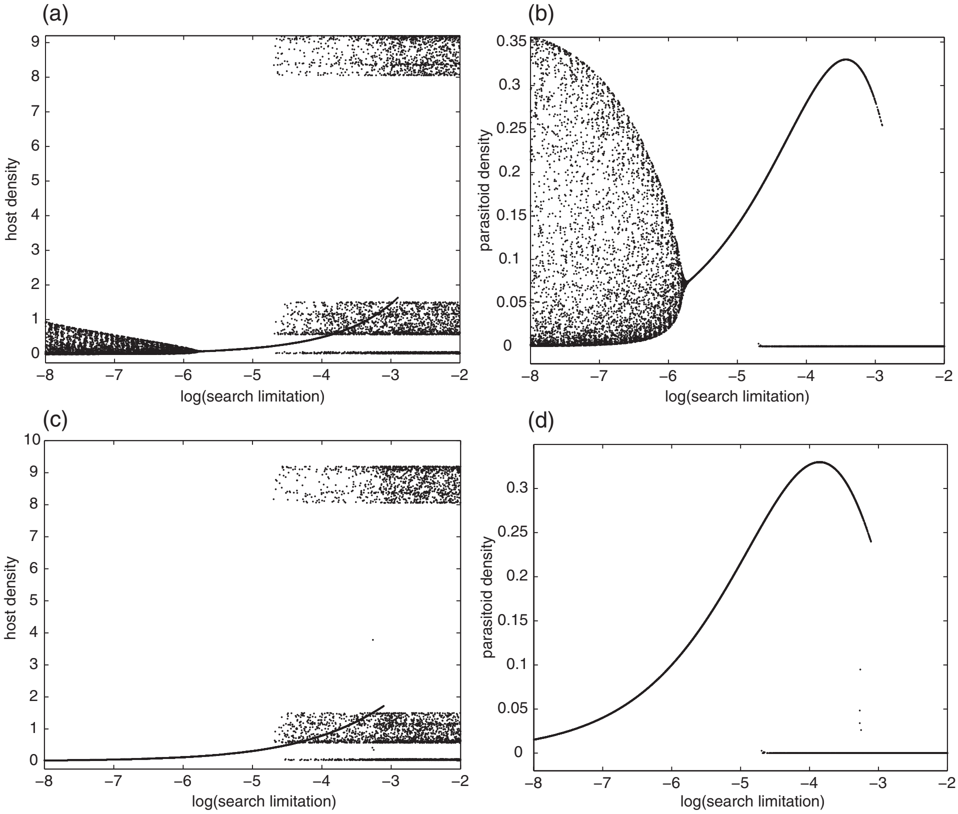

Figure 4. Effect of search limitation on host–parasitoid dynamics. In all figures, $f(N) = \exp(-N)$, $\lambda = 25$, $b = 0.01$, and $\theta = 1$. In (a) and (b), parasitoid attacks are less aggregated, i.e. $k = 1.1$. In (c) and (d), parasitoid attacks are more aggregated, i.e. $k = 0.9$.

mediates coexistence. The nature of this mediated coexistence depends critically on whether $k < 1$ or $k > 1$. When parasitoid attacks are mildly aggregated (i.e. $0.65 < k < 1$), weak search limitation results in hosts persisting stably at low densities. Alternatively, if parasitoid attacks are sufficiently random (i.e. $k > 1$), then weak search limitation mediates coexistence but the populations exhibit high-amplitude quasi-periodic dynamics. I conjecture that this difference stems from the fact that for sufficiently aggregated parasitic attacks (i.e. $k < 1$), parasitoid-driven extinction with $a = 0$ supports a stable equilibrium y_2^* for the dynamics of the parasitoid to host ratios. In contrast when parasitoid attacks are sufficiently random (i.e. $k > 1$), the parasitoid to host ratios diverge in the absence of search limitation.

The effects of increasing search limitation for $k > 1$ and $k < 1$ are illustrated in figure 4. This figure illustrates that increasing search limitation can initially stabilize the host–parasitoid dynamics. However, when search limitation is too severe, the parasitoids are unable to establish themselves. Interestingly, at intermediate levels of search limitation the realms of coexistence and parasitoid failure are intertwined: some initial conditions lead to parasitoid extinction while other initial conditions permit coexistence.

5. Discussion

There is an emerging consensus that parasitoids are egg-limited as well search-limited [10–12]. Egg limitation places a constraint on the maximal per-capita growth rate of the parasitoid. When hosts are not self-regulated (i.e. do not exhibit negative density-dependence), this constraint on parasitic growth tends to destabilize host–parasitoid interactions [4, 9]. Therefore, successful suppression of insect pests by parasitoids requires additional stabilizing mechanisms such as heterogeneity in the distribution of parasitic attacks or host density-dependence [1, 4, 14, 22]. To better understand how host density-dependence, heterogeneity in the distribution of parasitic attacks, and egg limitation influence host–parasitoid dynamics. I developed and analyzed difference equation models that account for all of these factors. Since successful agents of biological control are likely to be efficient in finding their hosts, the analysis and this discussion focuses on weakly search-limited parasitoids.

Although all parasitoids are search-limited, the analysis of purely egg-limited parasitoids provides a conceptual framework for understanding how egg limitation in of itself influences host–parasitoid dynamics. Based on prior work [20], the analysis reveals that parasitoids can invade the host system only if the parasitoid intrinsic fitness is greater than the host intrinsic fitness. Since the parasitoid intrinsic fitness is the expected number of progeny produced by a parasitoid that successfully lays all of its eggs, successful invasion of a parasitoid species requires that the ratio of the egg produced by the parasitoid to the eggs produced by the host is sufficiently large. When parasitoids can invade, the outcome of this invasion depends on the distribution of parasitoid attacks. In particular, there exists a critical threshold, call it CV^*, of the coefficient of variation (CV) of the number of parasitoid attacks per host. If $CV > CV^*$, then the parasitoid coexists with the host. This coexistence occurs typically (in a topological sense) about a periodic attractor. However, if $CV < CV^*$, then the parasitoid ultimately drives its host to extinction. The critical threshold CV^* is always greater than one. Hence, in a somewhat mysterious manner, these results connect to prior results about stability of the host–parasitoid equilibrium in the absence of host self-regulation. For instance, Hassell *et at.* [22] showed for a large class of models without egg limitation that $CV > 1$ is necessary and sufficient for stability. Alternatively, Getz and Mills [9] have shown that in the case of egg-limited encounter rates, $CV > 1$ is not sufficient for stability. Instead, the required CV for stability increases with the level of egg limitation. Analogously, it can be shown that the threshold value CV^* for the models considered here increases with the level of egg limitation. Hence, parasitoids with greater egg limitation require greater variation in the distribution of attacks to coexist with their hosts.

All parasitoids, of course, are search-limited. In the context of classical biological control, one would expect the most important parasitoids are those species which are weakly search-limited. The analysis of the weakly search limited model shows that coexistence occurs whenever the parasitoid intrinsic fitness exceeds the host intrinsic fitness. In particular, even when their attacks are randomly distributed (i.e. CV is small), the parasitoids are no longer able to over-exploit their hosts when they reach low densities. However, numerical simulations suggest that for hosts with highly unstable dynamics, there is a fundamental difference between $CV < 1$ and $CV > 1$ for the host–parasitoid dynamics. Parasitoid attacks that are too evenly distributed $(CV < 1)$ generate high-amplitude oscillations. In contrast, parasitoid attacks that are sufficiently but not overly aggregated (i.e. $CV > 1$ but close to 1) promote stability of host–parasitoid interactions and low host densities.

In conclusion, the analysis presented here suggests that parasitoid species with weak search limitation, sufficiently high egg loads relative to their hosts, and distributions of attack that are sufficiently but not overly aggregated are the best candidates for classical biological control.

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Appendix A. Proof of Theorem 3.2

Assume $k < 1$ and $a = 0$. Notice that $y_2^* = 0$ if $\theta < \lambda b$ and $y_2^* > 0$ if $\theta > \lambda b$. Define $\mathcal{A}_1 = \{(\lambda, \theta, b) \in (0, \infty)^3 : \theta > \lambda b\}$ and $\mathcal{A}_2 = \{(\lambda, \theta, b) \in (0, \infty)^3 : \theta < \lambda b\}$. By the analytic implicit function theorem and the definition of $y_2^* = y_2^*(\lambda, \theta, b)$, y_2^* varies analytically as a function of (λ, θ, b) on the open sets $\mathcal{A}_i$ with $i = 1, 2$. Consequently,

$$\mathcal{H}_i = \{x \longmapsto \lambda x \exp(-\alpha x) g(y_2^*) : (\lambda, \theta, b) \in \mathcal{A}_i\}$$

is an analytic family of maps. A straightforward calculation reveals the every $h \in \mathcal{H}_i$ has a unique critical point, x_c, and negative Schwartzian derivative (i.e. $h'''(x)/(h'(x)) - 3/2((h''(x))/(h'(x)))^2 < 0$ for all $x \neq x_c$). Moreover, since $\mathcal{H}_i$ contains maps with a globally attracting equilibrium as well as maps with period two points, there are at least two maps in $\mathcal{H}_i$ that are not combinatorially equivalent. Here, two maps h_1 and h_2 with critical points c_1 and c_2 are called combinatorially equivalent if there exists an order preserving bijection $F : \cup_{n\geq 0} h_1^n(c_1) \to \cup_{n\geq 0} h_2^n(c_2)$ such that $F(h_1^n(c_1)) = h_2^n(c_2)$ for all n. Based on these observations, the following remarkable theorem of Kozlovski [23] applies to $\mathcal{H}_i$. Prior to stating this theorem, recall that an invariant set $A \subset \mathbf{R}$ for a C^1 map $h : \mathbf{R} \to \mathbf{R}$ is *hyperbolic* if there exists $C > 0$, and $\lambda > 1$ such that $|f^{(n)}(x)| \geq C\lambda^n$ for all $x \in A$ and $n \geq 1$. A dissipative C^1 map $h : \mathbf{R} \to \mathbf{R}$ is *Axiom A* if h has a finite number of linearly stable periodic points and if the complement of the basin of attraction for these stable periodic points is hyperbolic. Dissipativity of h implies that if h is Axiom A, then h has at least one linearly stable periodic point (possibly of period 1).

THEOREM A1 (Kozlovski 2003 [23]) . *Let $\mathcal{H}$ be an analytic family of unimodal maps with a non-degenerate critical point and negative Schwartzian derivative. If there exist two maps in $\mathcal{H}$ that are not combinatorially equivalent, then there exists an open and dense subset $\mathcal{O}$ of $\mathcal{H}$ such that every $h \in \mathcal{O}$ is Axiom A.*

Let $\mathcal{B}_i$ with $i = 1, 2$ be the open and dense subset of parameters in $\mathcal{A}_i$ for which $h(x) = \lambda x \exp(-x) g(y_2^*)$ is Axiom A. Let (λ, θ, b) be in $\mathcal{B}_i$. Since h is unimodal with negative Schwartzian derivative, Singer's theorem [26] implies that there exists exactly one linearly stable periodic orbit. Moreover, the critical point for h lies in the basin of attraction of this stable periodic point. Now consider the map $H : \mathbf{R}_+^2 \to \mathbf{R}_+^2$ given by $H(y) = y'$ where y' is given by equation (3). If $\lambda g(y_2^*) < 1$, then Theorem 3.1 implies $y = (0, 0)$ is a periodic point of period 1 which attracts almost every initial condition. Now suppose that $\lambda g(y_2^*) > 1$. Theorem 3.1 implies that the line is $[0, \infty) \times \{y_2^*\}$ is a global attractor. The derivative matrix $DH(y)$ of $H(y)$ is an upper triangular matrix. Concavity of $1/g$ with $k < 1$ implies that $\partial H_2/\partial_{y2}(y_1, y_2^*) \in (0, 1)$ for all $y_1 \geq 0$. It follows for $(\lambda, \theta, b) \in \mathcal{B}_i$ with $\lambda g(y_2^*) > 1$, the map H is an Axiom A endomorphism (see [27] for a definition). Let $\Lambda \subset \mathbf{R}_+$ be the complement of the basin of attraction for the stable periodic orbit of h. Theorem 1 of [27] implies that the stables set of $\Lambda \times \{y_2^*\}$ for H has Lebesgue measure zero. Consequently, the basin of attraction of the stable periodic orbit has full Lebesgue measure for H. Taking $\mathcal{B}_1 \cup \mathcal{B}_2$ gives the desired open and dense set of parameters.

Appendix B. Proof of Theorem 4.1

Assume $a > 0$ and $\lambda > 1$. To prove this theorem, it suffices to translate some of my arguments on criteria for robust permanence for differential equations [28] to difference equations. For an alternative perspective on this approach, see the work of Garay and Hofbauer [29].

Define $F(N) = \lambda N f(N)$ and $G(N, P) = (F(N)g(E), \theta N f(N)(1 - g(E)))$ where $E = P/(a + bN)$. Iterating the maps $F(N)$ and $G(N, P)$ generate solutions to the host difference equation $N' = F(N)$ and the host–parasitoid difference equation $(N', P') = G(N, P)$, respectively. The first component G_1 of G can be expressed as $G_1(N, P) = Hh_1(N, P)$

where $h_1(N, P) = \lambda f(N)g(E)$. The second component G_2 of G can be expressed as $G_2(N, P) = Ph_2(N, P)$ where

$$h_2(N, P) = \begin{cases} \dfrac{G_2(N, P)}{P} & \text{if } P > 0 \\ \dfrac{\theta N}{a + bN} f(N) & \text{if } P = 0 \end{cases}$$

$h_2(N, P)$ is continuous as $G_2(N, P)$ is continuously differentiable and $G_2(N, 0) = 0$ for all $N \geq 0$. h_1 and h_2 are the per-capita growth rate (alternatively fitness) functions for the two species.

The assumptions that $\lim_{x\to\infty} f(x) = 0$ and $f(x)$ is decreasing imply there are $C < c < 0$ such that for all $N > 0$, $c \leq F^n(N) \leq C$ whenever n is sufficiently large. Let $\Lambda = \cap_{m\geq 0}\overline{\cup_{n\geq m} F^n([0, C])}$. Λ is the global attractor for F and has a Morse decomposition consisting of $\{0\}$ and

$$\Lambda^+ = \cap_{m\geq 0}\overline{\cup_{n\geq m} F^n(0, C])}.$$

Whenever the limit is defined, let

$$A(N) = \left\langle \frac{\theta F^n(N)}{a + bF^n(N)} \right\rangle_G$$

for any $N > 0$. Let $\mathcal{A} \subset [0, \infty)$ be the set of points such that $A(N)$ is well-defined. By the Birkhoff Ergodic Theorem, $\mathcal{A}$ forms a set of total probability, i.e. $\mu(\mathcal{A}) = 1$ for any F-invariant Borel probability measure.

Consider and F-invariant Borel probability measure μ. This measure is supported by Λ. Associated with the invariant measure are two Lyapunov exponents. The first exponent (in the host direction) is given by

$$\begin{aligned} L_1(\mu) &= \int_\Lambda \ln h_1(N, 0) \mathrm{d}\mu(N) \\ &= \ln \lambda + \int_\Lambda \ln f(N) \mathrm{d}\mu(N) \end{aligned}$$

where the second line follows from the fact that $g(0) = 1$. When μ is supported by Λ^+, $L_1(\mu) = 0$ (i.e. the average growth rate is zero) in which case $\int_\Lambda \ln f(N) d\mu(N) = -\ln \lambda$. When μ is supported by $\{0\}$ (i.e. μ is a Dirac measure on $\{0\}$) $L_1(\mu) = \ln \lambda$. The second Lyapunov exponent (the parasitoid invasion rate) is given by

$$\begin{aligned} L_2(\mu) &= \int_\Lambda \ln h_2(N, 0) \mathrm{d}\mu(N) \\ &= \int_\Lambda \ln f(N) \mathrm{d}\mu(N) + \int_\Lambda \ln \frac{\theta N}{a + bN} \mathrm{d}\mu(N) \end{aligned}$$

If μ is supported by Λ^+, then

$$L_2(\mu) = -\ln \lambda + \int_\mu \ln \frac{\theta N}{a + bN} \mathrm{d}\mu(N)$$

Hence, if μ is an ergodic probability measure supported by Λ^+, then the Birkhoff Ergodic Theorem implies that $\ln(A(N)/\lambda) = L_2(\mu)$ for μ almost every N.

Assume $A(N) > \lambda$ for all $N \in \mathcal{A} \cap (0, \infty)$. By the Birkhoff Ergodic Theorem, $L_2(\mu) > 0$ for all ergodic probability measures μ supported by Λ^+. On the other hand, since $\lambda > 1$, $L_1(\mu) = 0$ for the only probability measure μ supported by $\{0\}$. Translating the arguments found in [28, Theorem 4.3] for differential equations to difference equations implies that equation (1) is permanent.

Assume $A(N) < \lambda$ for some $N > 0$. Then there exists an ergodic probability measure μ supported by Λ^+ such that the transverse Lyapunov exponent $L_2(\mu)$ is negative. If G is twice continuously differentiable, that the Pesin Stable Manifold theorem (see, e.g., [30]) implies that there exists $N > 0$, $P > 0$ such that the second coordinate of $G^n(N, P)$ converges to zero as $n \to \infty$. In particular, equation (1) is not permanent.