J. Math. Biol. 52, 719–732 (2006)
Digital Object Identifier (DOI):
10.1007/s00285-005-0346-2

Mathematical Biology

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Host-parasitoid dynamics of a generalized Thompson model

Received: 14 June 2004 /

Abstract. A discrete-time host-parasitoid model including host-density dependence and a generalized Thompson escape function is analyzed. This model assumes that parasitoids are egg-limited but not search-limited, and is proven to exhibit five types of dynamics: host failure in which the host goes extinct in the parasitoid's presence or absence, unconditional parasitoid failure in which the parasitoid always goes extinct while the host persists, conditional parasitoid failure in the host and the parasitoid go extinct or coexist depending on the initial host-parasitoid ratio, parasitoid driven extinction in which the parasitoid invariably drives the host to extinction, and coexistence in which the host and parasitoid coexist about a global attractor. The latter two dynamics only occur when the parasitoid's maximal rate of growth exceeds the host's maximal rate of growth. Moreover, coexistence requires parasitism events to be sufficiently aggregated. Small additive noise is proven to alter the dynamical outcomes in two ways. The addition of noise to parasitoid driven extinction results in random outbreaks of the host and parasitoid with varying intensity. Additive noise converts conditional parasitoid failure to unconditional parasitoid failure. Implications for classical biological control are discussed.

1. Introduction

Parasitoids are insects, typically wasps or flies, whose larvae develop and kill their hosts, typically other insect species. Since parasitoids and their hosts have synchronized life-cycles, host-parasitoid dynamics are often described by difference equations. Thompson [30] in 1924 seems to have been the first to propose such a model for host-parasitoid interactions. To write down his model, Thompson made the following assumptions. Each host lays λ eggs per generation. Each parasitoid lays a eggs at random among a population of hosts i.e. parasitism events are Poisson distributed. If N is the density of hosts and P is the density of parasitoids, then the mean number of parasitoid eggs laid per host is aP/N, the fraction of hosts escaping parasitism is $\exp(-aP/N)$, and we arrive at Thompson's model:

$$\begin{aligned} N_{t+1} &= \lambda N_t \exp(-aP_t/N_t) \\ P_{t+1} &= N_t(1 - \exp(-aP_t/N_t)) \end{aligned}$$

Replacing $P_{t+1} = N_t(1 - \exp(-aP_t/N_t))$ with the approximation $P_{t+1} = aP_t$, Thompson showed that if $a > \lambda$ which in his words "c'est le seul cas pratiquement

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intéressant", then $\lim_{t\to\infty} N_t = 0$ whenever $P_0 > 0$. Thus, he concluded "malgré le fait que les oeufs sont distribués au hasard, le parasite finira par exterminer son hôte."

In 1935, Nicholson and Bailey [24] replaced Thompson's escape function $\exp(-aP_t/N_t)$ with $\exp(-bP_t)$ where b represents the parasitoid's searching efficiency. While Thompson's escape function assumes that parasitoids are egg limited but not search limited, Nicholson and Bailey's escape function assumes that parasitoids are search limited but not egg limited. However, all parasitoids experience search limitation and egg limitation to some degree. For instance, pro-ovigenic parasitoids which are born with a fixed compliment of eggs experience egg limitation whenever the number of hosts they encounter in their life time exceeds their complement of eggs [10]. On the other hand, 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 [10, 20].

Surprisingly, neither of these models permit equilibrium coexistence of hosts and parasitoids. The Thompson model admits no positive equilibrium, while the positive equilibrium of the Nicholson-Bailey model is unstable (see, e.g., [13,14]). Since the pioneering work of Thompson, Nicholson and Bailey, several mechanisms for stable coexistence have been found including aggregation of parasitoid attacks [10,13,22], host density dependence [3,23,32], density dependent sex ratios [5], and coevolution in spatially heterogenous environments [15,28,29,31]. Almost all of these papers are based on the Nicholson-Bailey escape function and have apparently lost sight of the Thompson escape function (see, however, [10,26]). The sparse attention paid to the Thompson escape function is surprising for several reasons. First, the Thompson escape function has the longest history of all host-parasitoid models. Second, the Thompson and Nicholson-Bailey models lie on the opposite ends of the egg-limited versus search-limited spectrum. While reality is likely to lie between the Nicholson-Bailey and Thompson extremes, understanding the dynamics at these extremes sheds light into the relative roles of search limitation and egg limitation on host-parasitoid dynamics. Third, ordinary differential equation models of ratio-dependent predation, the continuous time analog of (1), have been studied extensively in the past two decades [2,4,8,11,12,16,17,33]. These ratio-dependent models exhibit non-generic yet biologically realistic dynamics not observed in classical predator-prey models. One would expect similar dynamics in models with the Thompson escape function.

In this article, we consider a generalization of Thompson's model that includes host density dependence and aggregation of parasitoid attacks. This model assumes that parasitism (via the escape function $g(\cdot)$) occurs before density dependent mortality (via the survival function $f(\cdot)$) of the host (see, e.g., [15,23,32]):

$$\begin{aligned} N_{t+1} &= \lambda N_t f(N_t) g(P_t/N_t) \\ P_{t+1} &= \theta N_t f(N_t)(1 - g(P_t/N_t)) \end{aligned} \tag{1}$$

with $g(x) = (1 + ax/k)^{-k}$ or $g(x) = \exp(-ax)$. The escape function $g(x) = (1 + ax/k)^{-k}$ corresponds to negative binomially distributed parasitism events where

$k > 0$ is the negative binomial aggregation parameter. This choice of g is commonly used to model non-random or aggregated parasitism events [10, 13, 15, 22]. In the limiting case of $k = \infty$, this escape function simplifies to $g(x) = \exp(-ax)$. We analyze the global dynamics of (1) with and without additive noise. In section 2, analysis of the deterministic model reveals five types of global dynamics: parasitoid driven extinction, host failure, global coexistence, unconditional parasitoid failure, and conditional parasitoid failure. In section 3, we prove that additive noise fundamentally alters two of the dynamical outcomes: parasitoid driven extinction with noise results in random outbreaks of varying severity, and noise converts conditional parasitoid failure to unconditional parasitoid failure. In section 4, we discuss the implications of our results for biological control.

2. The dynamics of the generalized Thompson model

In this section, we consider the generalized Thompson model (1). About the host density dependent survival function f and the parasitism escape function g, we make the following assumptions:

H1 f is a continuous, non-increasing, positive function such that $f(0) = 1$ and $\lim_{x\to\infty} xf(x)$ exists (possibly infinite).

H2 $g(x) = (1 + ax/k)^{-k}$ with $k \in (0, \infty]$ where $k = \infty$ corresponds to $g(x) = \exp(-ax)$.

Permissible choices of f include no host density dependence with $f(N) \equiv 1$, the generalized Beverton-Holt function [9] $f(N) = \frac{1}{1+bN^c}$, or the Ricker [25] survival function $f(N) = \exp(-bN)$ where $b \geq 0$ and $c > 0$. Note that while (1) is not formally defined when $N_t = 0$, it extends continuously by defining $N_{t+1} = P_{t+1} = 0$ whenever $N_t = 0$.

Theorem 1. *The generalized Thompson model (1) satisfying* **H1**–**H2** *exhibits five types of dynamics:*

1. *(Host failure) If* $\lambda < 1$, *then*

$$\lim_{t\to\infty} (N_t, P_t) = (0, 0)$$

for any initial condition $N_0 > 0$ *and* $P_0 \geq 0$.

2. *(Parasitoid driven extinction and coexistence) If* $\lambda > 1$ *and* $\theta a > \lambda$, *then there exists* $k^* \in (0, 1)$ *and* $M > 0$ *such that*

$$\lim_{t\to\infty} (N_t, P_t) = (0, 0)$$

whenever $k > k^*$, $N_0 > 0$ *and* $P_0 > 0$, *and*

$$\liminf_{t\to\infty} N_t \geq M \qquad \liminf_{t\to\infty} P_t \geq M$$

whenever $k < k^*$, $N_0 > 0$ *and* $P_0 > 0$. *Moreover, for* $k \in (0, k^*)$ *there exists* y^* *(depending on* k*) such that*

$$\lim_{t\to\infty} P_t/N_t = y^*$$

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

3. *(Unconditional parasitoid failure) If* $\lambda > 1$, $\lambda > \theta a$ *and* $k \le 1$, *then there exists* $M > 0$ *such that*

$$\liminf_{t\to\infty} N_t \ge M \qquad \lim_{t\to\infty} P_t/N_t = 0$$

for any initial condition $N_0 > 0$ *and* $P_0 > 0$.

4. *(Conditional parasitoid failure) If* $\lambda > 1$, $\lambda > \theta a$, *and* $k > 1$, *then there exists* $y^* > 0$ *and* $M > 0$ *such that*

$$\lim_{t\to\infty} (N_t, P_t) = (0, 0)$$

whenever $P_0 > y^* N_0 > 0$, *and*

$$\lim_{t\to\infty} P_t/N_t = 0 \qquad \liminf_{t\to\infty} N_t \ge M$$

whenever $0 \le P_0 < y^* N_0$. *Moreover,* y^* *is a decreasing function of* $k > 1$.

This theorem proves that there are essentially five types of dynamics that (1) can exhibit. Host failure occurs when the host has insufficient reproductive capacity to sustain itself. Parasitoid driven extinction means that the introduction of a parasitoid unconditionally drives the host to extinction (Fig. 1a). Coexistence corresponds to the host and parasitoid persisting for all positive initial conditions. Moreover, in the case case of coexistence, the dynamics of (1) are asymptotic to

$$\begin{aligned} N_{t+1} &= \lambda N_t f(N_t) g(y^*) \\ P_t &= y^* N_t \end{aligned} \tag{2}$$

where y^* is the positive solution to $y = \frac{\theta}{\lambda}(1/g(y) - 1)$. Therefore, when the host dynamics are self limiting (i.e., $\lim_{N\to\infty} \lambda f(N) < 1$), standard arguments show coexistence corresponds to the existence of a global positive attractor (Fig. 1b and c). Parasitoid failure occurs when the host persists and the ratio of parasitoid to host goes to zero. Whenever the host exhibits self limitation, it can be easily shown that there exists $K > 0$ such that $\limsup_{t\to\infty} N_t \le K$. In which case, $\lim_{t\to\infty} P_t/N_t = 0$ and $\liminf_{t\to\infty} N_t \ge M$ imply that $\lim_{t\to\infty} P_t = 0$ (Fig. 1d). Finally, conditional parasitoid extinction requires that the parasitoid-host ratio be sufficiently high to ensure parasitoid driven extinction.

Proof. The proof relies on the following change of variables: $x_t = N_t$ and $y_t = P_t/N_t$ for $N_t > 0$. In this coordinate system, the dynamics of (1) become partially uncoupled:

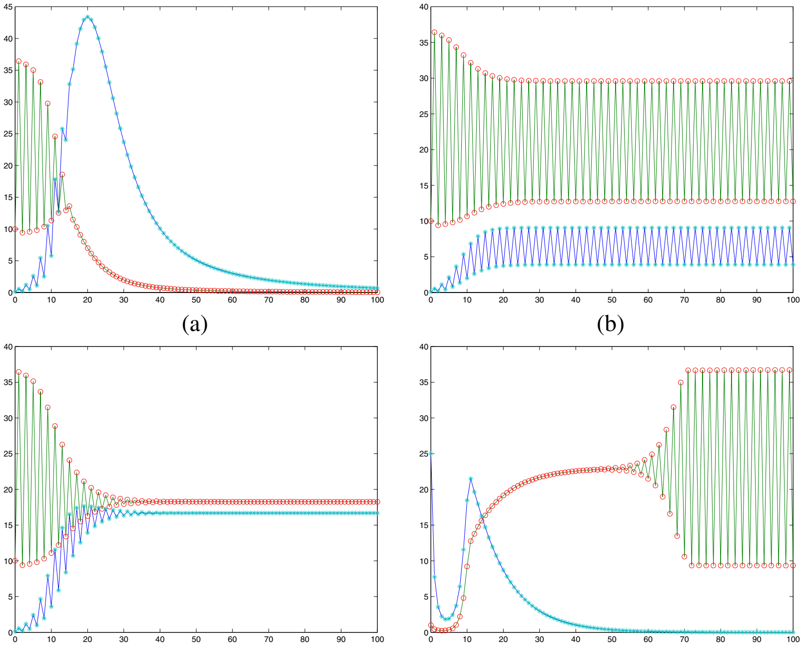
$$x_{t+1} = \lambda x_t f(x_t) g(y_t) \tag{3}$$

$$y_{t+1} = G(y_t) \tag{4}$$

where

$$G(y) := \frac{\theta}{\lambda}\left(\frac{1}{g(y)} - 1\right)$$

Since $g(y)$ is decreasing, $G(y)$ is an increasing function and any solution y_t to (4) converges to a fixed point (possibly $+\infty$) of G. Since $g(0) = 1$, $y = 0$ is always a fixed point of G. Moreover, $\lim_{y\to\infty} g(y) = 0$. To make use of these observations, we need the following lemma.



(a) (b)

(c) (d)

Fig. 1. Dynamics for (1) with $\lambda = 10.0$, $a = 1.0$, $f(N) = \exp(-0.1N)$. Host abundance is shown in red/green and parasitoid abundance in blue. In (a), parasitoid driven extinction occurs for the parameter values $k = 0.8$, $\theta = 15.0$ with the initial condition $(N_0, P_0) = (10, 0.1)$. In (b), host-parasitoid coexistence about a globally stable two-cycle occurs for the parameter values $k = 0.2$, $\theta = 15.0$ with the initial condition $(N_0, P_0) = (10, 0.1)$. In (c), host-parasitoid coexistence about a globally stable equilibrium occurs for parameter values $k = 0.4$, $\theta = 15.0$ with the initial condition $(N_0, P_0) = (10, 0.1)$. In (d), parasitoid failure occurs for the parameter values $k = 0.9$, $\theta = 9$ with the initial condition $(N_0, P_0) = (1, 25)$.

Lemma 1. *Let* $\lambda > 0$. *Suppose* y_t *is a solution to (4) and* $y^* := \lim_{t\to\infty} y_t$ *(possibly* $+\infty$*). If* $\lim_{t\to\infty} \lambda g(y_t) < 1$, *then*

$$\lim_{t\to\infty} x_t = 0$$

for any solution x_t *to (3) with* $x_0 \geq 0$. *If* $\lim_{t\to\infty} \lambda g(y_t) > 1$, *then there exist* $M > 0$ *such that*

$$\liminf_{t\to\infty} x_t \geq M$$

for any solution x_t *to (3) with* $x_0 > 0$.

Proof. Let y_t be a solution to (4) and define $y^* = \lim_{t\to\infty} y_t$ and $g^* = \lim_{t\to\infty} g(y_t)$. Suppose $\lambda g^* < 1$. Choose $\epsilon > 0$ such that $\rho := \lambda(g^* + \epsilon) < 1$. Since $\lim_{t\to\infty} y_t = y^*$, there exists $T > 0$ such that $\lambda g(y_t) \leq \rho$ for all $t \geq T$. Since $f(x_t) \leq 1$ for all t, we have $x_{t+1} \leq \rho x_t$ for $t \geq T$ and $\lim_{t\to\infty} x_t = 0$. Suppose $\lambda g^* > 1$. Choose

$\epsilon > 0$ sufficiently small so that $\varrho := \lambda(g^* - \epsilon) > 1$. Define $F_1(x) = \lambda x f(x)$ and $F_2(x) = \varrho x f(x)$. Since $\lim_{t\to\infty} y_t = y^*$, there exists $T_1 > 0$ such that $\lambda g(y_t) \geq \varrho$ for all $t \geq T_1$. Since f is continuous and $f(0) = 1$, we can choose $\delta > 0$ such that $\varrho f(x) > 1$ for $x \in [0, \delta]$. Define $\alpha = \inf\{F_2(x) : x > \delta\}$. Suppose $\alpha > 0$. Let $M = \min\{\alpha, \delta\}$. Since $F_2(x) > x$ for $x \in (0, M]$ and $x_{t+1} \geq F_2(x_t)$ for $t \geq T_1$, there exists $T_2 \geq T_1$ such that $x_{T_2} \in [M, \infty)$. Since $F_2([M, \infty)) \subset [M, \infty)$ and $x_{t+1} \geq F_2(x_t)$ for all $t \geq T_1$, we get $x_t \in [M, \infty)$ for all $t \geq T_2$. Now, suppose that $\alpha = 0$. Since F_2 is positive and continuous, $\alpha = 0$ and **H1** imply that $\lim_{x\to\infty} F_2(x) = \lim_{x\to\infty} F_1(x) = 0$. Let $x^* = \sup\{x : F_1(x) = x, x > 0\}$. Since $F_1(x) > x$ on $(0, \delta]$ and $\lim_{x\to\infty} F_1(x) = 0$, we get $x^* \in (\delta, \infty)$. Define $\gamma = \max\{F_1(x) : x \in [0, x^*]\}$. Since $F_1(x^*) = x^*$, we get $\gamma \geq x^* > \delta$. Define $\xi = \min\{F_2(x) : x \in [\delta, \gamma + 1]\}$ and $M = \min\{\delta, \xi\}$. Since $F_2(x) < F_1(x) < x$ for $x > \gamma$, we have $F_1([M, \gamma+1]) \subset [M, \gamma+1)$ and $F_2([M, \gamma+1]) \subset [M, \gamma+1)$. Recall that $F_2(x_t) \leq x_{t+1} \leq F_1(x_t)$ for all $t \geq T_1$. Hence, if $x_{T_2} \in [M, \gamma + 1]$ for some $T_2 \geq T_1$, then $x_t \in [M, \gamma + 1]$ for all $t \geq T_2$ and we are done. It remains to show that there exists such a $T_2 \geq T_1$. If $x_{T_1} \in [M, \gamma + 1]$, we define $T_2 = T_1$. Next suppose $x_{T_1} \in (0, M)$. Since $F_2(x) > x$ for $x \in (0, M]$, $F_1(x) \leq \gamma$ for all $x \in (0, M)$, and $F_1(x_t) \geq x_{t+1} \geq F_2(x_t)$ for $t \geq T_1$, there exists $T_2 \geq T_1$ such that $x_{T_2} \in [M, \gamma + 1]$. Finally, suppose $x_{T_1} > \gamma + 1$. Since $F_1(x) < x$ for $x > \gamma$ and $x_{t+1} \leq F_1(x_t)$ for all t, there exists $T_3 > T_1$ such that $x_{T_3} \in (0, \gamma + 1)$. If $x_{T_3} \in [M, \gamma + 1]$, we are done. If $x_{T_3} \in (0, M)$, we apply the preceding argument to get a $T_2 > T_3$ such that $x_{T_2} \in [M, \gamma + 1]$. □

Using the preceding lemma, we can prove the main statements of the Theorem. First, consider the case $\lambda < 1$. Let (x_t, y_t) be a solution to (3)-(4) with $x_0 > 0$ and $y_0 \geq 0$. Since $f(x) \leq 1$ and $g(x) \leq 1$ for all $x \geq 0$, $x_{t+1} = \lambda x_t f(x_t) g(y_t) \leq \lambda x_t$ for all t. Hence, $\lim_{t\to\infty} x_t = 0$. Since $P_{t+1} \leq \theta x_t$ for all $t \geq 0$, we have $\lim_{t\to\infty} P_t = 0$.

Second, consider the case $\lambda > 1$ and $\theta a > \lambda$. Suppose $k \geq 1$. Let (x_t, y_t) be a solution to (3)–(4) such that $x_0 > 0$ and $y_0 > 0$. Since $G(y)$ is convex when $k \geq 1$ and $G'(0) = \theta a/\lambda > 1$, we get $G(y) > y$ for $y > 0$ and $\lim_{t\to\infty} y_t = \infty$. Since $\lim_{t\to\infty} \lambda g(y_t) = 0$, Lemma 1 implies $\lim_{t\to\infty} x_t = 0$. Suppose $k < 1$. Then $G(y)$ is concave and $\lim_{y\to\infty} G(y)/y = 0$. Since $G'(0) = \theta a/\lambda > 1$, these observations imply that $G(y)$ has a unique positive fixed point y^*. Moreover, $G(y) > y$ for $y < y^*$ and $G(y) < y$ for $y > y^*$. Therefore, $\lim_{t\to\infty} y_t = y^*$. If $\lambda g(y^*) > 1$, Lemma 1 implies that there exists $M > 0$ (independent of x_0 and y_0) such that $\liminf_{t\to\infty} x_t \geq M$. Since $y_t = P_t/N_t$, we get $\liminf_{t\to\infty} P_t \geq M y^*$. Alternatively, if $\lambda g(y^*) < 1$, Lemma 1 implies that $\lim_{t\to\infty} x_t = 0$. Since $P_{t+1} \leq \theta x_t$ for all $t \geq 0$, we have $\lim_{t\to\infty} P_t = 0$. To find the critical value $k = k^*$, let $y^*(k) > 0$ denote the unique positive solution to $G(y) = y$ for any $k \in (0, 1)$. We will show that for any $y > 0$, $G(y)$ is an increasing function of k. From this fact and concavity of G when $k \leq 1$, it follows that $y^*(k)$ is an increasing function of $k \in (0, 1)$. Indeed, we have

$$\frac{\partial G}{\partial k} = \frac{\theta}{\lambda} \frac{(1 + ay/k)^k h(y)}{k + ay}$$

where $h(y) = -ay + (k + ay)\ln(1 + ay/k)$. Hence, the sign of $\frac{\partial G}{\partial k}$ is determined by the sign of $h(y)$. Since $h(0) = 0$ and $h'(y) = a\ln(1 + ay/k) > 0$ for all $y > 0$, we get that $h(y) > 0$ for all $y > 0$. Hence, $y^*(k)$ increases with $k \in (0, 1)$. Moreover, $\lim_{k\to 0} y^*(k) = 0$ and $\lim_{k\to 1} y^*(k) = \infty$. Since $\lambda g(0) = \lambda > 1$ and $\lim_{y\to\infty} \lambda g(y) = 0$, there is a $k^* \in (0, 1)$ such that $\lambda g(y^*(k)) > 1$ for $k \in (0, k^*)$ and $\lambda g(y^*(k)) < 1$ for $k \in (k^*, 1)$.

Third, consider the case $\lambda > 1, \theta a < \lambda$, and $k \le 1$. Let (x_t, y_t) be a solution to (3)–(4) such that $x_0 > 0$ and $y_0 \ge 0$. Since $G(y)$ is concave and $G'(0) = \theta a/\lambda < 1$, we get $G(y) < y$ for all $y > 0$. Hence, $\lim_{t\to\infty} y_t = 0$. Lemma 1 implies that there exists $M > 0$ (independent of x_0 and y_0) such that $\liminf_{t\to\infty} x_t \ge M$.

Finally, consider the case in which $\lambda > 1, \theta a < \lambda$, and $k > 1$. Let (x_t, y_t) be a solution to (3)–(4) such that $x_0 > 0$ and $y_0 > 0$. Since $G(y)$ is convex, $G'(0) < 1$, and $\lim_{y\to\infty} G(y)/y = \infty$, there exists a unique positive fixed point y^* for G. Moreover, convexity implies that $G(y) < y$ whenever $y < y^*$ and $G(y) > y$ whenever $y > y^*$. Suppose $y_0 > y^*$. Then $\lim_{t\to\infty} y_t = \infty$. Lemma 1 implies that that $\lim_{t\to\infty} x_t = 0$. Since $P_t \le \theta x_t$ for all t, $\lim_{t\to\infty} P_t = 0$. Suppose that $y_0 < y^*$. Then $\lim_{t\to\infty} y_t = 0$. Lemma 1 implies that there exists $M > 0$ (independent of x_0 and $y_0 > y^*$) such that $\lim_{t\to\infty} x_t \ge M$. Note that since G is convex and increasing with respect to k (see argument in second case), y^* decreases as k increases. □

When we have more information about $f(N)$, it is possible to provide much stronger results about the dynamics of (1). For instance, the following corollary follows immediately from Theorem 1 and the observation that the Beverton-Holt map $F(x) = \frac{\lambda x}{1+bx}$ with $b > 0$ has a globally stable fixed point given by $\frac{\lambda-1}{b}$ whenever $\lambda > 1$ and given by 0 whenever $\lambda \le 1$.

Corollary 1. *Suppose $f(N) = 1/(1 + bN)$ with $b > 0$, $\lambda > 1$ and* **H2** *holds. Then (1) exhibits the following dynamics:*

1. *(Parasitoid driven extinction and global stability) If $\lambda > 1$ and $\theta a > \lambda$, then there exists $k^* \in (0, 1)$ and $M > 0$ such that for $k > k^*$*

$$\lim_{t\to\infty} (N_t, P_t) = (0, 0)$$

whenever $N_0 > 0$ and $P_0 > 0$, and for $k < k^*$ there exists a positive equilibrium $(\hat{N}, \hat{P})$ such that

$$\lim_{t\to\infty} (N_t, P_t) = (\hat{N}, \hat{P})$$

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

2. *(Parasitoid failure) If $\lambda > \theta a$ and $k \le 1$, then*

$$\lim_{t\to\infty} (N_t, P_t) = (\frac{\lambda - 1}{b}, 0)$$

for any initial condition $N_0 > 0$ and $P_0 > 0$

3. *(Conditional parasitoid failure) If* $\lambda > 1$, $\lambda > \theta a$, *and* $k > 1$, *then there exists* $y^* > 0$ *and* $M > 0$ *such that*

$$\lim_{t\to\infty}(N_t, P_t) = (0, 0)$$

whenever $P_0 > y^* N_0 > 0$, *and*

$$\lim_{t\to\infty}(N_t, P_t) = (\frac{\lambda - 1}{b}, 0)$$

whenever $0 < P_0 < y^* N_0$.

3. Generalized Thompson dynamics with additive noise

In this section, we consider the effect of small additive noise on the dynamics of the generalized Thompson model. More specifically, we consider

$$\begin{aligned} X_{t+1} &= \max\{\lambda X_t f(X_t) g(Y_t/X_t) + \epsilon W_{t+1}, 0\} \\ Y_{t+1} &= \max\{\theta X_t f(X_t)(1 - g(Y_t/X_t)) + \epsilon Z_{t+1}, 0\} \end{aligned} \tag{5}$$

where W_t and Z_t are i.i.d. random variables uniformly distributed on $[-1, 1]$ and $\epsilon > 0$. When $X_t = 0$, we interpret these equations as $X_{t+1} = \max\{\epsilon W_t, 0\}$ and $Y_t = \max\{\epsilon Z_t, 0\}$. One can view this noise as corresponding to small random events of immigration and mortality. With this form of noise, Ruelle's work [27] on random perturbations of dynamical systems allows us to characterize several aspects of the dynamics of (5). A nice account of Ruelle's work can be found in Kifer's book [18].

For expositional purposes, we shall assume that density-dependent survival is of the form $f(N) = \frac{1}{1+bN}$. Define

$$F(N, P) = \begin{cases} (\lambda N f(N) g(P/N), \theta N(1 - g(P/N)) & \text{if } N > 0 \\ (0, 0) & \text{else} \end{cases}$$

and let F^t denote F composed with itself t times.

Theorem 2. *Let* $f(N) = \frac{1}{1+bN}$, *g be given by* **H2**, k^* *be as defined in Theorem 1,* $\lambda > 1$ *and*

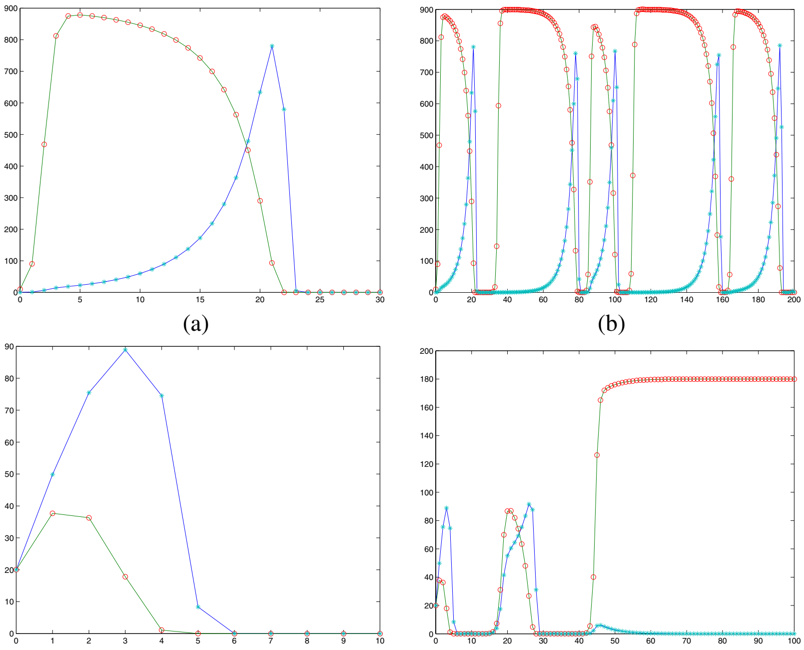
$$A = \bigcap_{t\geq 0}\{F^t(N, P) : 0 \leq N \leq (\lambda - 1)/b, 0 \leq P \leq \theta(\lambda - 1)/b\}$$

Assume $(X_0, Y_0) \in A$ *and* $X_0 Y_0 > 0$. *Then*

1. *(Coexistence) If* $\theta a > \lambda$ *and* $k < k^*$, *then there exists a unique positive equilibrium* $(\hat{N}, \hat{P})$ *for (1) such that for any open neighborhood U of* $(\hat{N}, \hat{P})$

$$P(\textit{there exists } T > 0 \textit{ s.t. } (X_t, Y_t) \in U \textit{ for all } t \geq T) = 1$$

whenever $\epsilon > 0$ *is sufficiently small.*



(a) (b)

(c) (d)

Fig. 2. Dynamics for the noisy Thompson model (5) with $\lambda = 10.0$, $a = 1.0$, $f(N) = 1/(1 + bN)$, and $k = 20$. Host abundance is shown in red/green and parasitoid abundance in blue. In (a) and (b), $b = 0.01$, $\theta = 12$, and $(N_0, P_0) = (10, 0.1)$. In (c) and (d), $b = 0.05$, $\theta = 8$, and $(N_0, P_0) = (20, 20)$. In (a) and (c), the dynamics without any noise (i.e. $\epsilon = 0$) correspond to unconditional and condition parasitoid driven extinction, respectively. In (b) and (d), a small amount of additive noise (i.e. $\epsilon = 0.01$) to the deterministic models yields repeated outbreaks and unconditional failure, respectively.

2. *(Repeated outbreaks) If* $\theta a > \lambda$ *and* $k > k^*$*, then for any open set* $U \subset A$

$$P((X_t, Y_t) \text{ enters } U \text{ infinitely often }) = 1$$

whenever $\epsilon > 0$ *sufficiently small.*

3. *(Parasitoid failure) If* $\theta a < \lambda$*, then for any neighborhood* U *of* $((\lambda - 1)/b, 0)$

$$P(\text{there exists } T \text{ s.t. } (X_t, Y_t) \in U \text{ for } t \geq T) = 1$$

whenever $\epsilon > 0$ *is sufficiently small*

Several of the implications of Theorem 2 are illustrated in Figs. 2 and 3. Figs. 2a and 2b illustrate that injecting noise in the case of parasitoid driven extinction leads to random outbreaks of hosts and parasitoids. While these repeated outbreaks spend most of their time near the unstable manifolds of the equilibria (0, 0) and (900, 0), they eventually fully explore the global attractor A of (1) (see Fig. 3). Figs. 2c and 2d illustrates that additive noise converts conditional parasitoid failure to unconditional parasitoid failure.

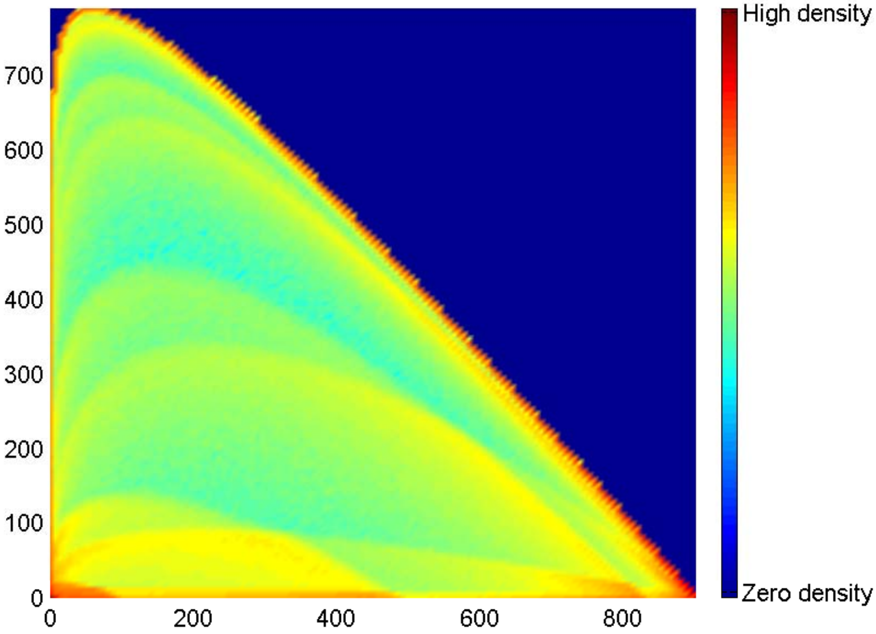


Fig. 3. Asymptotic density for the noisy Thompson model (1) with repeated outbreaks. Using parameters and initial conditions described in Fig. 2b, the model is iterated 25,000,000 generations. A histogram of these iterations is plotted in a 135 × 135 grid in the host-parasitoid plane with cooler and warmer tones corresponding to lower and higher densities, respectively.

In order to prove Theorem 2, we need to recall a few definitions from dynamical systems. Let $\|(N, P)\| = |N|+|P|$. A sequence $(N_0, P_0), \ldots, (N_t, P_t)$ of elements in $\mathbf{R}^2_+$ such that $\|(N_{i+1}, P_{i+1}) - F(N_i, P_i)\| < \epsilon$ for all $i \in \{0, \ldots, t-1\}$ is called an ϵ *pseudo orbit of* F *of length* t. A point x is *chain recurrent* if for every $\epsilon > 0$ and every $t > 0$ there is an ϵ pseudo orbit of length $\geq t$ going from x to x. Using pseudo orbits, one can define a partial ordering on $\mathbf{R}^2_+$ and a corresponding equivalence relation. For $x, y \in \mathbf{R}^2_+$ define $x \succeq y$ (‘x *chains to* y’) if for every $\epsilon > 0$ there exists an ϵ pseudo orbit going from x to y. Define $x \sim y$ if $x \succeq y$ and $y \succeq x$. The equivalence class of x under $\sim$ is denoted as $[x]$. An equivalence class $[x]$ is called a *quasi-attractor* if x is chain recurrent and $x \succeq y$ implies that $y \in [x]$. A compact set A is an *attractor* if $F(A) = A$ and there exists a neighborhood U of A such that $\cap_{t\geq 0} F^t(U) = A$.

Proof. Since $A = \bigcap_{t\geq 0}\{F^t(N, P) : 0 \leq N \leq (\lambda - 1)/b, 0 \leq P \leq \theta(\lambda - 1)/b\}$ is the global attractor of (1), there exist nested compact neighborhoods $V_1 \subset V_2$ of A and $\epsilon_0 > 0$ such that there exist no ϵ_0-pseudo orbits starting in V_1 and ending in

$\mathbf{R}^2 \setminus V_2$. Since $(X_0, Y_0), \ldots, (X_t, Y_t)$ is an ϵ pseudo orbit for all t and $(X_0, Y_0) \in A$, we get that $(X_t, Y_t) \in V_2$ for all t whenever $0 < \epsilon < \epsilon_0$.

Suppose that $\theta a > \lambda$ and $k < k^*$. Corollary 1 implies that there is a globally stable equilibrium $(\hat{N}, \hat{P})$ for (1). Let U_2 be a neighborhood of $(\hat{N}, \hat{P})$. Since $(\hat{N}, \hat{P})$ is an attractor, there exists a compact neighborhood $U_1 \subset U_2$ of $(\hat{N}, \hat{P})$ and $\epsilon_1 \in (0, \epsilon_0)$ such that there are no $\epsilon_1 > 0$ pseudo-orbits from U_1 to $\mathbf{R}^2_+ \setminus U_2$. Since $(\hat{N}, \hat{P})$ is the only quasi-attractor for (1), Theorem 4.5 in Kifer [18] implies that with probability one there exists T (a random stopping time) such that $(X_T, Y_T) \in U_2$. Since $(X_T, Y_T), \ldots, (X_{T+t}, Y_{T+t})$ is an ϵ-pseudo orbit for all $t \geq T$, (X_{T+t}, Y_{T+t}) remains in U_2 for all $t \geq T$ provided that $0 < \epsilon < \epsilon_1$.

Suppose that $\theta a > \lambda$ and $k > k^*$. The equilibrium $(\frac{\lambda-1}{b}, 0)$ is globally stable for (1) restricted to N-axis. Moreover, $\lim_{t\to\infty}(N_t, P_t) = (0, 0)$ whenever $P_0 > 0$ and $N_0 > 0$. Hence, $x \succeq y$ for all $x, y \in A$ i.e. A is a quasi-attractor. Let any open set $U \subset A$ be given. For any $x \in V_2$ and $\epsilon > 0$, there exists an ϵ pseudo orbit of length t_x from x to a point in U. By compactness of V_2, we can choose the ϵ pseudo orbits such that there exists $\bar{t}$ with $t_x \leq \bar{t}$ for all $x \in V_2$. Equation (4.15) in [18, Theorem 4.5] implies that there exists $\alpha = \alpha(\epsilon) > 0$ such that $P((X_{t_x}, Y_{t_x}) \in U | (X_0, Y_0) = x) \geq \alpha$ for all $x \in V_2$ and $\epsilon > 0$. Since $(X_t, Y_t) \in V_2$ for all $t \geq 0$, a standard result in Markov chain theory (see e.g. Theorem 2.3 in Chapter 5 in [7]) implies that

$$P((X_t, Y_t) \text{ enters } U \text{ infinitely often}) = 1$$

whenever $0 < \epsilon < \epsilon_0$.

Suppose that $\lambda > \theta a$. The only quasi-attractor is the linearly stable equilibrium $(\hat{N}, 0) = (\frac{\lambda-1}{b}, 0)$. Let U_2 be a neighborhood of $(\frac{\lambda-1}{b}, 0)$. Since $(\frac{\lambda-1}{b}, 0)$ is an attractor, we can find a neighborhood $U_1 \subset U_2$ and $\epsilon_1 \in (0, \epsilon_2)$ such that there is no ϵ_1 pseudo orbit from U_1 to $\mathbf{R}^2_+ \setminus U_2$. Since $(\frac{\lambda-1}{b}, 0)$ is the only quasi-attractor, Theorem 4.5 in Kifer [18] implies that with probability one there exists T (a random stopping time) such that $(X_T, Y_T) \in U_1$. On the other hand, since $(X_T, Y_T), \ldots, (X_{T+t}, Y_{T+t})$ define ϵ pseudo-orbits for (1), (X_t, Y_t) remains in U_2 for $t \geq T$ provided that $0 < \epsilon < \epsilon_1$. □

4. Discussion

In this paper, we investigated a host-parasitoid model with an parasitism escape function introduced by Thompson [30]. This escape function assumes that parasitoids are egg limited but not search limited. Our analysis proves that the deterministic model exhibits five types of dynamics which we now interpret in the context of classical biological control where the host is a pest ideally eradicated by the parasitoid. When the host has a maximal growth rate of less than one (i.e. $\lambda < 1$), the host is not a pest and both species decline deterministically to extinction. For the remainder of the discussion, we assume the host is a pest and has a maximal growth rate greater than one. The remaining four dynamical behaviors fall into two classes. In the first class, the maximal growth rate of the host exceeds the maximal growth rate of the parasitoid (i.e. $\lambda > \theta a$). If the parasitoid attacks are sufficiently aggregated (i.e. $k \leq 1$), then unconditional parasitoid failure occurs:

for all initial conditions the parasitoid goes extinct, while the host persists. If the parasitoid attacks are sufficiently random (i.e. $k > 1$), then the parasitoid can drive the host deterministically to extinction provided that the initial parasitoid-host ratio exceeds a critical threshold. This critical threshold decreases with the aggregation parameter k. Hence, successful biological control is most likely if the distribution of parasitoid attacks is sufficiently random. In the second class of dynamical outcomes, the maximal growth rate of the parasitoid exceeds the maximal growth rate of the host. From Thompson's perspective, "c'est le seul cas de pratiquement intéressant" as it is the only time the parasitoid can unconditionally regulate the host. If the parasitoid attacks are sufficiently random (i.e. $k > k^*$ where $k^* < 1$), then the parasitoid deterministically drives the host to extinction whenever they are introduced into the system. This prediction is consistent with the work of Getz and Mills [10] who simulated (1) with $f \equiv 1$ and concluded "that under some circumstances, highly search-efficient parasitoids are able to drive the host population to extinction, even if they only have a finite number of eggs to lay." Finally, if the parasitoid attacks are sufficiently aggregated (i.e. $k < k^*$), then the host and parasitoid coexist about a global attractor. If the host has self-limiting dynamics that are not overcompensating (e.g. Beverton-Holt model), then coexistence occurs about a globally stable equilibrium. Moreover, the host's equilibrium abundance can be arbitrarily small provided that the parasitoid has a sufficiently high egg load (i.e. a is sufficiently large) or is sufficiently gregarious (i.e. θ is sufficiently large). Hence, the generalized Thompson model resolves the "paradox of biological control" in which according to the classical predator-prey theory, you can not have both a low and stable prey equilibrium density [1,21].

Since the generalized Thompson model has a ratio-dependent escape function, it is not surprising that it exhibits similar dynamics to differential equation models of ratio-dependent predation [4,16,17,19,33]. However, these two dimensional ordinary differential equation models can not exhibit chaotic behavior. The generalized Thompson model, on the other hand, can exhibit chaotic dynamics when the host experiences overcompensating density dependence such as Ricker survival $f(N) = \exp(-bN)$ or generalized Beverton-Holt survival $f(N) = \frac{1}{1+bN^c}$ with $c > 1$. For these choices of density dependence, chaotic coexistence or parasitoid failure culminating in chaotic host dynamics can be proven to occur using equation (2) and the theory of one-dimensional maps [6].

We proved that additive noise can substantially change the long-term behavior of these ratio-dependent systems. When the underlying deterministic dynamics correspond to conditional parasitoid failure, additive noise results in unconditional parasitoid failure: if the parasitoid drives the host toward extinction, small levels of additive noise can dramatically decrease the parasitoid-host ratio and result in parasitoid failure. When the underlying deterministic dynamics correspond to parasitoid driven extinction, additive noise results in repeated outbreaks of the host and the parasitoid. Moreover, even for small levels of noise, the outbreaks will vary randomly in severity from mild to extreme. Alternatively, when the underlying deterministic dynamics correspond to global coexistence or unconditional parasitoid failure, small levels of additive noise have virtually no effect on the long-term behavior of the system. These results suggest that for biological control there is a trade off between low host abundance and susceptibility to a host outbreak due to a random event decreasing the parasitoid-host ratio.

In conclusion, the generalized Thompson model exhibits biologically realistic dynamics not exhibited by their Nicholson-Bailey counterparts. While some of these dynamics are noise sensitive, many of their their features are like to persist in other models with escape functions accounting for egg-limitation. For instance, Rogers [26] (see also [10,13]) introduced an escape function, $g(N, P) = \exp(-abP/(a+bN))$, that simultaneously accounts for egg and search limitation. Roger's escape function converges to the Nicholson escape function as $a \uparrow \infty$ and converges to Thompson's escape function as $b \uparrow \infty$. When search limitation is mild, Roger's model numerically exhibits similar dynamics to the Thompson model [10]. However, a complete understanding of the dynamics of (1) with Roger's escape function is likely to provide significant mathematical challenges.

Acknowledgements. This work was supported in part by National Science Foundation Grants DMS-0517987 and E F-0436318.

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