A remark on "Biological control through provision of additional food to predators: A theoretical study" [Theor. Popul. Biol. 72 (2007) 111–120]

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ABSTRACT

Biological control, the use of predators and pathogens to control target pests, is a promising alternative to chemical control. It is hypothesized that the introduced predators efficacy can be boosted by providing them with an additional food source. The current literature (Srinivasu, 2007; 2010; 2011) claims that if the additional food is of sufficiently large quantity and quality then pest eradication is possible in *finite* time. The purpose of the current manuscript is to show that to the contrary, pest eradication is *not possible* in finite time, for *any* quantity and quality of additional food. We show that pest eradication will occur only in infinite time, and derive decay rates to the extinction state. We posit a new modeling framework to yield *finite* time pest extinction. Our results have large scale implications for the effective design of biological control methods involving additional food.

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1. Introduction

1.1. Overview

The combination of species introductions (both intentional and accidental), and changing habitats due to human activity, has led to a growing number of invasive species worldwide (Pimentel et al., 2005; Paini et al., 2016; Lewis et al., 2016; Jongejans et al., 2011). The development and implementation of successful control strategies for these pest species is crucial. Control and even eradication has been successful in some cases (Paini et al., 2016), but we are still losing ground as the number of new invasive species recorded annually continues to grow (now at a rate of over 500 new species per year; Seebens et al., 2017), with no indication of things slowing down. Normally benign native species can also become destructive pests when humans alter environments, for example by farming crops in large monocultures (Wetzel et al., 2016).

Chemical pesticides have been used heavily to control and eliminate pest species an estimated 500 million kg is applied annually in the United States alone (Pimentel and Burgess, 2014). This has been used heavily against corn insects, such as in the state of Iowa and the Midwest in general, where losses due to the European corn borer and Western corn rootworm alone, amount to in excess of \$3 billion annually (Lundgren et al., 2015; Sappington, 2014; Lundgren and Fergen, 2014). However, chemical pesticides can have a variety of negative environmental and human health impacts. One alternative is deployment of biological control agents — natural enemies of the pest species (Van Driesche and Bellows, 1996; Czaja et al., 2015; Bampfylde and Lewis, 2007; Kang D. Bai et al., 2017; Snyder and Wise, 1999). The effects of antagonistic ecological interactions (i.e. a predator eating animal pests, an herbivore eating plant pests, or pathogens infecting both animal and plant pests) are qualitatively similar — one species negatively impacts the other while benefiting from the interaction.

The benefits of using a biological control approach are that it is non-toxic and can be self-sustainable. Once introduced, a successful predator population can grow and reproduce, removing the need for the repeated applications often required with the use of chemical pesticides (Bampfylde and Lewis, 2007; Van Driesche and Bellows, 1996). However, there are also potential drawbacks, including the possibility for insufficient predation pressure resulting in incomplete eradication of the pest species and the potential for ecological and/ or evolutionary shifts that result in expected species interactions (Sabelis and Van Rijn, 2006; Friman et al., 2014). One approach when the introduced predator does not sufficiently reduce pest density, is to try and boost predator efficiency by supplementing the system with an

additional food source for the predator. Food supplementation has been tested in a range of field studies, sometimes leading to significant reductions in numbers of pests (pests declined in 28 of the 59 trials reviewed in Wade et al., 2008), but rarely is complete elimination reported. There has been many investigations into factors that may determine the efficacy of the food supplementation (Canas and O'Neil, 1998; Evans and Swallow, 1993; Shannon et al., 2007; Saunders et al., 2010; Wetzel et al., 2016; Tena et al., 2015; Rosenheim et al., 1995; Tena et al., 2015; Evans and Swallow, 1993; Sabelis and Van Rijn, 2006; Evans and Richards, 1997) but there is no clear consensus in the biological literature, as to why or why not this approach works.

A number of mathematical models that describe predator-pest dynamics with an additional food source have been developed, stemming from three key papers in the literature, starting with Srinivasu et al. (2007) and continued in Srinivasu and Prasad (2010) and Srinivasu and Prasad (2011). In these works the dynamics of an introduced predator depredating on a target pest, whilst it is provided with an additional food source is introduced. This is modeled by the following non-dimensionalized system (Srinivasu et al., 2007),

$$
\begin{aligned}
\frac{dx}{dt} &= x(1 - \frac{x}{\gamma}) - \frac{xy}{1 + \alpha\xi + x}, \\
\frac{dy}{dt} &= \frac{\beta xy}{1 + \alpha\xi + x} + \frac{\beta\xi y}{1 + \alpha\xi + x} - \delta y.
\end{aligned} \tag{1}
$$

Here $x(t), y(t)$ are non-dimensionalized measures of the number/density of pest and predator species divided by the half saturation constant of the functional response in the original model. γ is the carrying capacity of the pest, again relative to the original half saturation constant, β is the conversion efficiency of the predator relative to the maximum birth rate of the pest, δ is the death rate of the predator again relative to the maximum birth rate of the pest, $\frac{1}{\alpha}$ is the quality of the additional food provided to the predator. Essentially $\frac{1}{\alpha} = \frac{h_1}{h_2}$, where h_1 is the predators handling time for the pest, and h_2 is the predators handling time for the additional food. Thus high quality additional food (or $\frac{1}{\alpha}$ being large) corresponds to h_2 being much smaller than h_1 — that is the predator is able to handle the additional food much faster than the target pest. ξ is the quantity of additional food provided to the predator, again relative to the half saturation constant. See Srinivasu et al. (2007) for further description of the non-dimensionalization of these parameters. Note, $\gamma, \beta, \delta, \alpha, \xi$ are all positive constants. We provide the details behind the derivation of the functional response for the above model in (7)–(9).

In Srinivasu et al. (2007) it is claimed that (1) can facilitate pest extinction in finite time. We quote from Srinivasu et al. (2007),

"*Originally, if the ecosystem supports coexistence of prey and predators (i.e., the system (1) admits an interior equilibrium point whether stable or unstable) then continuous supply of high-quality additional food to the predators with the supply level $\xi \in [0, \frac{\delta}{\beta - \delta\alpha}]$ decreases the equilibrium prey population from $\frac{\delta}{\beta - \delta}$. Increasing the additional food supply beyond this interval **eradicates the prey from the ecosystem in a finite time**, and from that time the predators survive only on the external food supply*". The above claim is however not proved until Srinivasu and Prasad (2011). The above results are highly promising for the field of biological control, as they show a modification to the classic Rosenzweig–McArthur model, via the introduction of additional food can cause pest eradication. Thus these results have led to much research activity recently (Srinivasu et al., 2007; Srinivasu and Prasad, 2010, 2011; Chakraborty et al., 2017; Srinivasu et al., 2018). The quantity $\beta - \delta\alpha$, comes up from the form of the equilibrium solutions to (1). Here $x(\xi) = \frac{\delta - (\beta - \delta\alpha)\xi}{\beta - \delta}$. Thus for positivity of equilibrium we

require, $\frac{\delta}{\beta - \delta\alpha} > \xi > 0$, and so we require $\beta - \delta\alpha > 0$. If $\xi > \frac{\delta}{\beta - \delta\alpha}$, there is no interior equilibrium, and only a pest free equilibrium exists, seen from the form of the nullclines of (1), Srinivasu et al. (2007) and Srinivasu and Prasad (2011). Biologically, $\beta - \delta\alpha > 0$ can be interpreted as $\frac{1}{\alpha} > \frac{\delta}{\beta}$, or that the quality of additional food should be greater than the ratio of deaths to births in the system, for there to exist a feasible interior equilibrium — and for the possibility for additional food mediated pest extinction. That is if $\frac{1}{\alpha} < \frac{\delta}{\beta}$, then pest extinction via additional food is not possible, see Lemma 2.1.

In the current manuscript we show that pest eradication via (1), is *not possible* in finite time, even if the quantity of additional food satisfies, $\xi > \frac{\delta}{\beta - \delta\alpha}$. This is shown via Theorem 2.2. We also show pest eradication in finite time is not possible even in the limit that $\xi \to \infty$, or in the limit that $\alpha \to 0$. That is for any arbitrarily high quantity or quality of additional food, via Proposition 1. Note, additional food can however cause pest eradication in *infinite* time. Decay rates to the extinction state are derived via Lemma 5.1. Lastly we propose a new model for finite time pest extinction via (15)–(16). The finite time extinction results are demonstrated via Theorem 2.3 and Corollary 1. We also show that under certain choice of parameters the pest free equilibrium is globally attracting, via Theorem 2.4.

2. Finite time extinction

2.1. Constant quantity of additional food

We recap the result of interest from the literature which quantifies the efficacy of the predator to achieve pest eradication when supplemented with additional food via (1),

Lemma 2.1 (*cf. Lemma 1 from Srinivasu and Prasad, 2011; Srinivasu et al., 2007*).

(a) If the quality of the additional food satisfies $\beta - \delta\alpha > 0$, then prey can be eradicated from the ecosystem in a finite time by providing the predator with additional food of quantity $\xi > \frac{\delta}{\beta - \delta\alpha}$.

(b) If the quality of the additional food satisfies $\beta - \delta\alpha < 0$, then it is not possible to eradicate prey from the ecosystem through provision of such additional food to the predators.

Remark 1. Notice if $\xi = 0$, or there is no additional food (1) reduces to the classical Rosenzweig–McArthur predator–prey model, for which we know prey eradication *is not possible*, as the only prey free state is $(0, 0)$, which is unstable.

Note, Lemma 2.1 is not quite accurate. That is for a constant quantity of additional food, pest extinction does not occur in *finite* time. We state this via the following theorem,

Theorem 2.2. *Consider the predator-pest system described via* (1). *Pest eradication is not possible in finite time even if the quality of the additional food satisfies $\beta - \delta\alpha > 0$ and the quantity of the additional food satisfies $\xi > \frac{\delta}{\beta - \delta\alpha}$.*

Pest extinction is however possible in infinite time. We derive decay rates to this end,

Proposition 1. *Consider the predator-pest system described via* (1), *and assume we remain in the region of the phase defined by*

$$y \geq x + 1 + \alpha\xi, \tag{2}$$

then if the pest is driven to the extinction state, for an arbitrarily large quantity ξ of additional food, this occurs at best at the super exponential rate

$$x_0 e^{-e^{\left(\frac{\beta}{\alpha} + \beta\right)t}} \leq x(t). \tag{3}$$
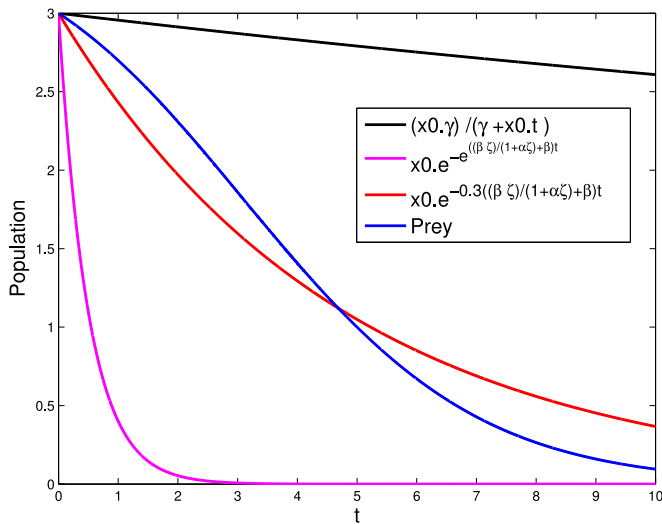
Fig. 1. We simulate (1) with $\beta = 0.4, \delta = 0.3, \gamma = 200, \xi = 7.6, \alpha = 1.2$. Here $\xi = 7.6 > 7.5 = \frac{0.3}{0.4-(0.3)(1.2)} = \frac{\delta}{\beta-\delta\alpha}$. Thus according to Lemma 2.1 from Srinivasu et al. (2007) and Srinivasu and Prasad (2011) pest eradication is possible in a finite time. We pick initial conditions $x_0 = 3, y_0 = 14$. This ensures that the initial data satisfies the condition of Proposition 1.

Also, if the pest is driven to the extinction state, for an arbitrarily high quality $\frac{1}{\alpha}$ of additional food, this occurs at best at the super exponential rate

$$x_0 e^{-e^{(\beta\xi+\beta)t}} \leq x(t). \tag{4}$$

These decay estimates are compared to the polynomial and super exponential decay rates derived in Lemma 5.1 in 1. We also compare them to an exponential decay rate. We see from the simulations therein that the decay rate of the pest to the extinction state is closer to super exponential than polynomial. This decay rate however depends on the choice of parameters. Thus for different parameters it could be closer to a polynomial/exponential decay.

2.2. The foraging time of a predator

In this section we recap certain pertinent classical theory on the foraging time of predators. This will provide a transition into our new modeling formulation. The classical theory of "time budget" in ecology (Kuang, 2007) assumes that a predator spends its time on two kinds of activities:

- Searching for prey
- Handling prey: chasing, killing, eating and digesting.

The predators total foraging time T equals the sum of time spent on searching T_s and time spent on handling T_h. Assume that a predator captures H_a prey during time T. Handling time is proportional to the number of prey captured, so $T_h = H_a h$. Where h is time spent on handling of one prey. We also assume that a predator searches area a (search rate) per unit of time and catch a fixed proportion ρ of all prey in there. Let x be the prey density, then $T_s = \frac{H_a}{a\rho x}$, and standard ecological theory (Kuang, 2007) yields the classical type II functional response,

$$p(x) = \frac{a\rho x}{1 + a\rho h x} \tag{5}$$

There is a consensus in the literature that provision of additional food will increase the total time T that the predator spends in foraging, as there now is a component T_a, which is the time that

goes to handling the additional food (Srinivasu et al., 2007, 2018),

$$T_a = \frac{H_a}{a\rho x} h\xi\alpha \tag{6}$$

The handling time of the additional food is directly proportional to its quantity ξ (more additional food − longer it will take to handle) and inversely proportional to its quality (note quality is $\frac{1}{\alpha}$, so lower quality food will take longer to handle and digest).

However the overall handling time is now $T_h + T_a$. Thus the overall foraging time now is,

$$T = T_s + T_h + T_a = \frac{H_a}{a\rho x} + H_a h + \frac{H_a}{a\rho x} h\xi\alpha \tag{7}$$

and hence

$$H_a = \frac{a\rho x T}{1 + h\xi\alpha + a\rho h x} \tag{8}$$

This gives the functional response used in the current literature (Srinivasu et al., 2007; Srinivasu and Prasad, 2010, 2011)

$$p(x) = \frac{H_a}{T} = \frac{a\rho x}{1 + h\xi\alpha + a\rho h x} \tag{9}$$

The above functional response looks similar to the Holling type II response. However, its significance is in the $h\xi\alpha$ term that appears in it. This enables the vertical predator nullcline to be moved closer and closer to the y-axis, by increasing ξ the quantity of additional food. Then finally over to coincide with the y-axis which yields a prey free state. For any value of ξ greater than this (that is if $\xi > \frac{\delta}{\beta-\delta\alpha}$ (Srinivasu et al., 2007; Srinivasu and Prasad, 2011)) one will only have a prey free state, while the predator can survive on additional food. This mechanism is not possible without the additional food ξ.

2.3. A new modeling formulation

We present a new modeling formulation next. We define T_{ha}, as the time that goes to handling the target pest in the presence of additional food, and T_{sa}, the time that goes into searching for the target pest in the presence of additional food. Also, the assumption in the literature is that the predator does not spend any time in searching for the additional food itself (Srinivasu and Prasad, 2010, 2011).

We make the following assumptions,

Assumption 1. The predator will spend the same time T on foraging, with or without the additional food. That is,

$$T_{sa} + T_{ha} + T_a \approx T_s + T_h \tag{10}$$

Assumption 2. The additional food does not have an effect on the predators handling time of the pest, so $T_{ha} = T_h$. Since $T_a \geq 0$, via (10) we have,
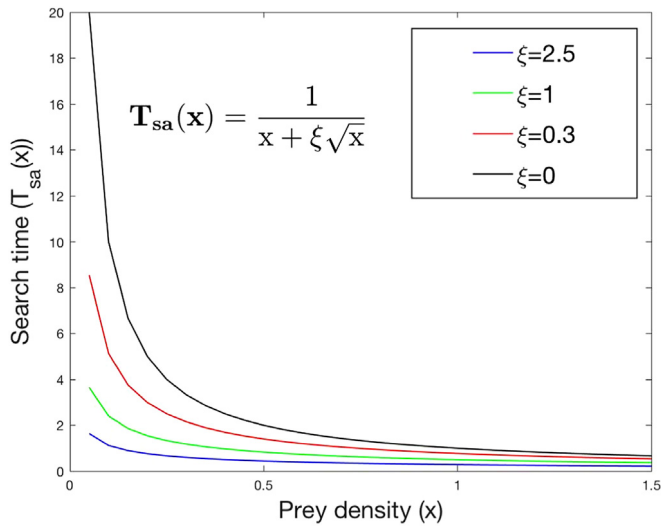
$$T_{sa} \leq T_s \tag{11}$$

We conjecture,

Conjecture 1. *The additional food ξ lowers the predators search time for the pest,*

$$T_{sa}(x, \xi) = \frac{H_a}{a\rho(f(x, \xi))} \leq \frac{H_a}{a\rho x} = T_s(x), \tag{12}$$

where $f(x, \xi) \geq x$, and $f(x, 0) = x$. The effect of ξ is pronounced at low pest density, and declines at higher pest densities, so $(T_s - T_{sa})$, is a monotonically decreasing function of pest density x. Also,

$$\lim_{x\to\infty}(T_s - T_{sa}) \to 0. \tag{13}$$

Fig. 2. The search time T_{sa} is shown across a range of pest densities. We show three different search times, for varying amounts of additional food ξ. We also compare to the model with no additional food ($\xi = 0$).

Fig. 3. Here we are plotting the curves via (44) to partition the space of initial data into those which led to finite time blow up/finite time extinction vs those which do not.

See Fig. 2 where we show the search time T_{sa} as a function of pest density, and the effect of additional food on it. We also compare it to T_s. Essentially, at low pest density, the additional food model ($\xi > 0$) shows a shorter search and higher pest consumption rate compared to the model without additional food ($\xi = 0$). Higher ξ, shortens search times, but this is most pronounced at low pest densities, and less pronounced at higher pest densities. That is $(T_s - T_{sa}) \to 0$ as $x \gg 1$. Note the search times are not continuous at $x = 0$, and that $x = 0$ is a vertical asymptote for the search times. This intuitively means that the predators search times get infinitely large in the limit of vanishing prey.

We are not certain about what the most realistic form of f should be biologically. We are merely positing that there is an effect of the additional food ξ on decreasing the predators search time, and this can be modeled via an f, that does not necessarily depend linearly on pest density x. Note, various f have been proposed in the ecological literature, advocating that in certain situations search time does not decrease linearly with increasing prey density (McKenzie et al., 2012; Ruxton, 2005; Mols et al., 2004). In order to determine the precise feedback between the additional food and the pest density, we will have to perform species specific laboratory experiments such as in Ruxton (2005).

However, if one assumes $T_{sa}(x) = \frac{H_a}{a\rho(f(x,\xi))}$, and follows standard optimal foraging theory such as via (7)–(9), so that $\left(\frac{\text{energy intake}}{\text{foraging time}}\right)$ is maximized, then the functional response that is derived is,
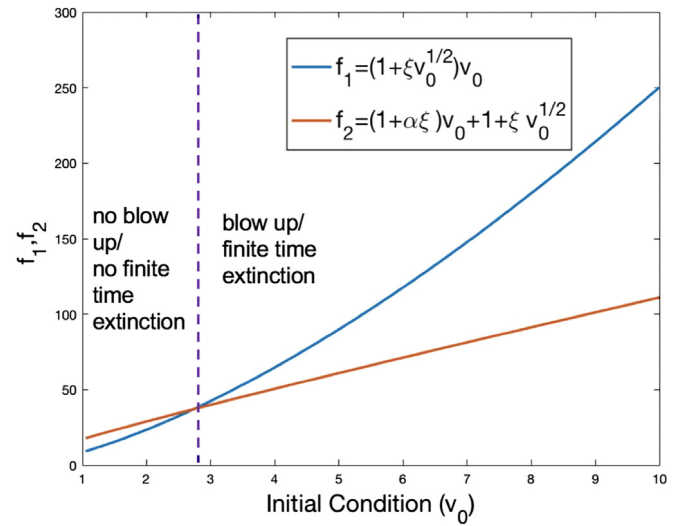
$$p(x) = \frac{H_a}{T} = \frac{a\rho f(x, \xi)}{1 + h\xi + a\rho h f(x, \xi)} \tag{14}$$

Thus, given a search time as in (12), where $f(x, \xi) = x + \xi g(x)$, following standard theory (Křivan, 1996), one obtains the corresponding predator pest system,

$$\frac{dx}{dt} = x(1 - \frac{x}{\gamma}) - \frac{(x + \xi g(x))y}{1 + \alpha\xi + (x + \xi g(x))}, \tag{15}$$

$$\frac{dy}{dt} = \frac{\beta(x + \xi g(x))y}{1 + \alpha\xi + (x + \xi g(x))} + \frac{\beta\xi y}{1 + \alpha\xi + (x + \xi g(x))} - \delta y. \tag{16}$$

Remark 2. Theoretically, for $f(x, \xi) = x + \xi g(x)$, $g(x)$ could be a variety of sub-linear functions, for finite time extinction to occur, such as $g(x) = \sqrt{x}$. See Theorem 2.3 and Corollary 1.

Theorem 2.3. *Consider the predator-pest system described via* (15)–(16). *For any set of parameters, there exist a sufficiently large initial condition y_0, and a sufficiently small initial condition x_0, for which pest eradication is possible in finite time.*

We next state a corollary that follows,

Corollary 1. *Consider* (15)–(16). *If $g(v)$ satisfies,*

$$\left(1 + \xi v g\left(\frac{1}{v}\right)\right)v^p > (1 + \alpha\xi)v + 1 + \xi v g\left(\frac{1}{v}\right), \tag{17}$$

for $v = \frac{1}{x} \gg 1$, $0 < p < 1$, then x the solution to (15) *will go extinct in finite time for suitably small initial data x_0. Such a g is necessarily sub linear (see Fig. 3).*

2.4. Dynamics of new model

In this section we demonstrate that the predator-pest system described via (15)–(16) exhibits a variety of dynamics. We choose $\alpha = 1, \beta = 0.4, \gamma = 6, \delta = 0.3$, and vary the quantity of additional food ξ. Our choice of parameter values is biologically motivated in that we clearly want a higher intrinsic growth rate of the predator, than death rate, so $\beta > \delta -$ whilst maintaining a moderate carrying capacity level γ. The choice of $\alpha = 1$, modulates ξ to be in the range $[0, 3]$ for an interior equilibrium to exist. Given that $\gamma = 6$, a maximum of $\xi = 3$ would be approximately half the carrying capacity at most, which is biologically realistic (Czaja et al., 2015; Sabelis and Van Rijn, 2006; Wade et al., 2008).

We notice that various dynamics are possible in ranges of ξ. For $0 < \xi < 0.2$, there exists an interior equilibrium which is locally stable. This is shown in Fig. 4. For larger initial conditions, we see that the pest free equilibrium is reached in finite time. When we increase ξ beyond 0.2, the interior equilibrium loses stability, and a limit cycle appears. This happens through a Hopf bifurcation. We see this numerically via computing eigenvalues when $\xi = 0.18$, the interior equilibrium is a spiral sink and the eigenvalues are $-0.0031385 + 0.1966i$ and $-0.0031385 + 0.1966i$. We then compute eigenvalues when $\xi = 0.22$. Now the interior equilibrium is a spiral source and the eigenvalues are $0.0089257 + 0.19656i$ and $0.0089257 - 0.19656i$, and so the
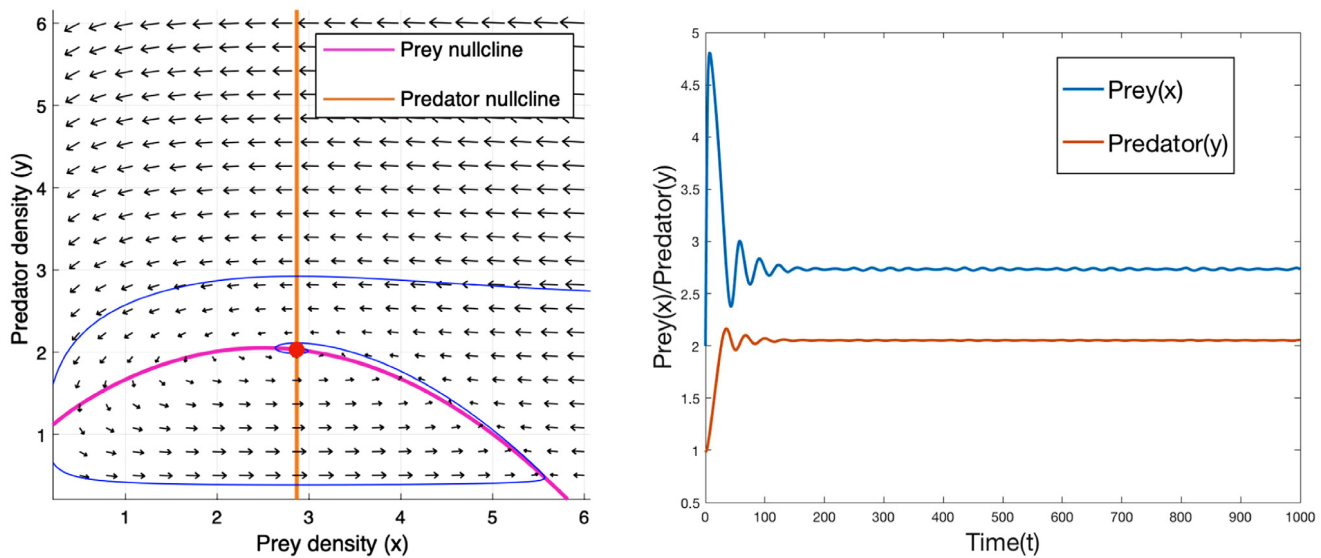
Fig. 4. We see the phase plot and corresponding time series for via (15)–(16) when $0 < \xi < 0.2$. There exists a locally stable interior equilibrium as well as a pest extinction state.
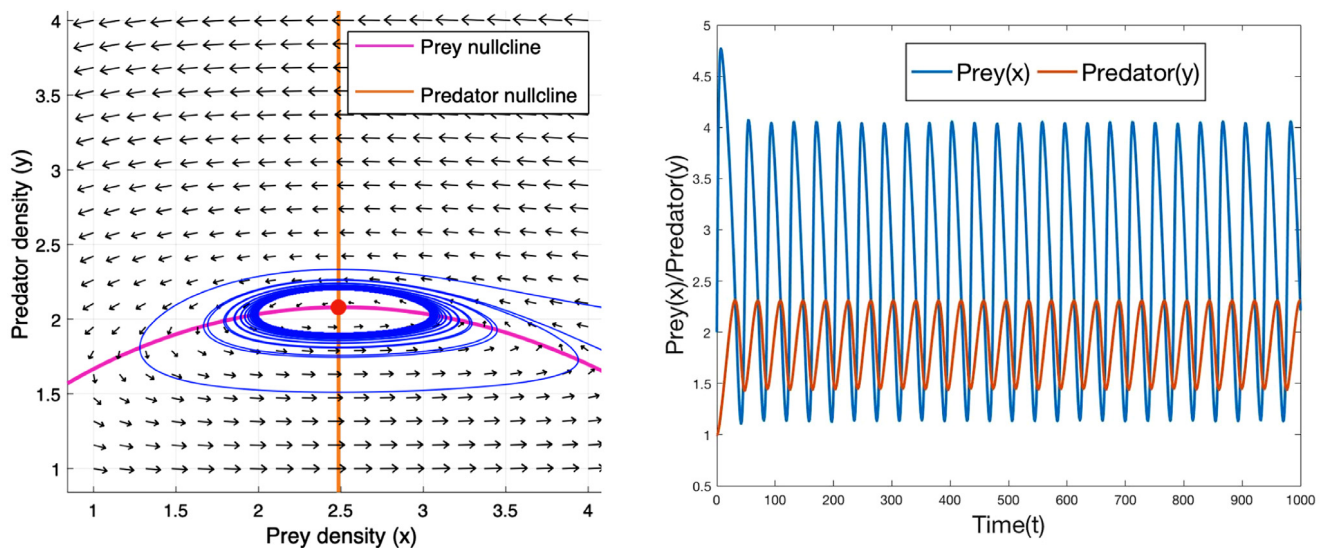
Fig. 5. We see the phase plot and corresponding time series for via (15)–(16) when $0.2 < \xi < 1$. There now exists a limit cycle as well as a pest extinction state.

eigenvalues have crossed the real axis from negative to positive as the parameter ξ is varied in the range [.18, .22]. The trajectories spiral out of the unstable equilibrium and onto the stable limit cycle, which has formed as a result of a super critical Hopf bifurcation. This is seen via Fig. 5. Pest extinction in finite time still occurs for larger initial conditions.

Next, as we increase ξ beyond 1, the limit cycle disappears, there is an interior equilibrium, but it is unstable. Thus the pest extinction state becomes globally attracting. This is seen via Fig. 6. Increasing ξ beyond 3 causes this interior unstable equilibrium to disappear, and we only have the pest extinction state which is globally attracting.

We next state a global stability result, for the pest free equilibrium.

Theorem 2.4. *Consider the predator-pest system described via* (15)–(16). *There exist parameter values for which the pest free equilibrium is globally stable, as long as g(x) satisfies the condition in* (17).

3. Discussion and conclusions

We have shown for a constant quantity of additional food, pest eradication is not possible in finite time no matter how large the quantity or how high the quality of the additional food is. However, with the introduction of additional food the pest population can be reduced to very small numbers, and in a real biological population, this may turn out to be sufficient. Populations with a small numbers of individuals are often subject to increased demographic stochasticity, leading to high likelihoods of extinction (Percus, 2005) despite their continuous deterministic dynamics suggesting otherwise. Future exploration of models that include stochasticity could help to determine how the likelihood of eradication changes in the presence of additional food when small population processes are considered. Alternatively, since a constant quantity of additional food cannot yield finite time eradication of the pest, some amount of stochasticity could even cause pest rebound. Proving conditions under which this might occur can also make for an interesting future direction.
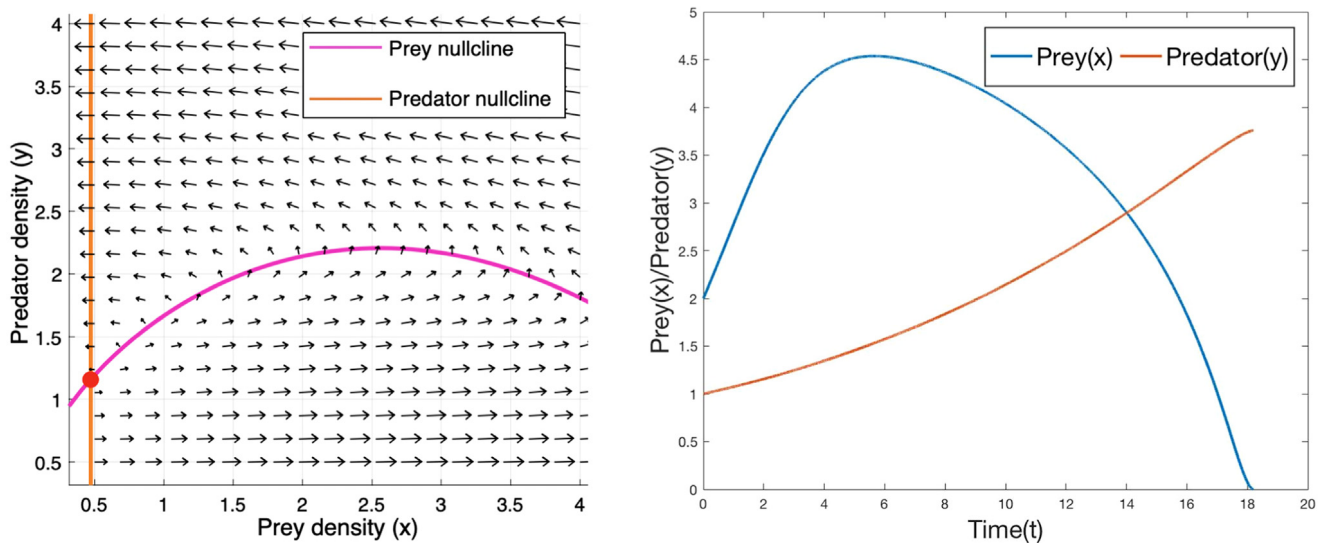
Fig. 6. We see the phase plot and corresponding time series for via (15)–(16) when $1 < \xi$. There now exist an unstable interior equilibrium and a pest extinction state.

Our alternate modeling framework suggests a way in which additional food could result in finite time pest extinction. This new framework relies on the assumption that predators spend a fixed amount of time foraging for food and when additional food is provided, predators adjust the amount of time they spend searching for the pest. This adjustment results in shorter pest search time and so higher pest consumption rates at low pest density. A few studies suggest that this type of functional response can be appropriate in some real systems (McKenzie et al., 2012; Mols et al., 2004; Ruxton, 2005; Ioannou et al., 2008), and lab experiments are currently under way to explore this possibility further. The specific biological mechanisms that might drive this kind of non-linear relationship between prey density and handling time are not clear, but rely on deviations from modeling predators and prey as simply random moving particles that bump into each other at some rate proportional to their density. Instead, predators and/or prey adjust their predation and escape behaviors respectively and these behavioral changes then impact encounter rates. An example that might work in the context of our model might be predators moving (and so searching) more quickly when their energy has been boosted by consumption of a secondary type of food. In a study characterizing stickleback fish searching and consuming invertebrate prey, Ioannou et al. (2008), found that stickleback tend to increase their searching speed the longer they go without encountering prey. Further observational and experimental studies are required to identify more behavioral changes that have the potential to impact search time.

Another interesting direction would be to derive our predator-pest system, using the classical optimal foraging theory in the setting of one predator — two prey (Křivan, 1996; Krivan, 2010), where the second prey item would be the additional food. However, in this framework, the handling time of the preys does not depend on each other. In our assumed frame work, we assume the additional food *influences* the handling time of target prey, and working to verify this possibility both theoretically and via laboratory experiments, are the subject of current and future investigations. Note that if we allow a very large amount of additional food to be input into the system, it is unreasonable to expect that the predator will continue to focus on the target pest. Thus a reasonable assumption here may be to restrict the range of ξ, so as to be in tune with the classical one predator — two prey optimal foraging theory. Phase analysis shows that the predator-pest system (15)–(16), derived via our new modeling framework

has a variety of interesting dynamics. A pest free equilibrium is certainly possible for small values of γ and large values of ξ — and under certain parametric restrictions this can be globally attracting. A future direction of interest is a complete dynamical analysis of this system, exploring the various intermittent dynamics and bifurcations as we vary all the other parameters of interest. In particular it would be useful to calculate the separatrix dividing the phase space into trajectories that converge to the interior equilibrium or limit cycle, versus those that converge to the pest free state. It would also be interesting to derive parametric restrictions under which the pest free equilibrium is globally attracting (see Fig. 6).

Regardless of the mode by which this is applied in real systems, a key to pest eradication seems clear — increase per capita prey consumption rates when the pest population size is low. In this regard, exploration of other functional forms for the density-dependent food supplementation may prove fruitful, particularly ones that describe changes in predator handling and searching behavior that depend on pest and/ or additional food densities.

Mathematical models of biocontrol can provide an idea of what dynamics are possible and suggest routes by which pest eradication is theoretically feasible. Future directions involve studying the effects of pest refuge, evolutionary effects as well as stochastic effects (Parshad et al., 2016a; Krivan, 2010; Percus, 2005; Bailey et al., 2013, 2015; Friman et al., 2014; Parshad et al., 2016b; Hawkins et al., 1993). However, experimental tests are required to assess the biological reality of applying these strategies. Laboratory experiments using dynamically interacting predator (protozoa), prey (bacteria), and additional food (a chemical supplement) are currently underway and will help to provide an additional intermediate step linking theory to successful biocontrol applications in the natural world.

Acknowledgment

Appendix

Proof of Theorem 2.2. We proceed by contradiction. Assume the following parametric restrictions on the quality and quantity of

additional food are satisfied, $\beta - \delta\alpha > 0$, $\xi > \frac{\delta}{\beta - \delta\alpha}$, and the pest x goes extinct in finite time. Then

$$\lim_{t \to T^* < \infty} x(t) \to 0. \tag{18}$$

Now consider the state variable v, defined by $v = \frac{1}{x}$. We must have

$$\lim_{t \to T^* < \infty} v(t) \to \infty. \tag{19}$$

or v must blow up in finite time (Quittner and Souplet, 2007; Parshad et al., 2017). A simple substitution $v = \frac{1}{x}$ in (1) yields the following new system for the states v and y.

$$\begin{aligned}
\frac{dv}{dt} &= -v + \frac{1}{\gamma} + \frac{yv^2}{1 + (1 + \alpha\xi)v} \\
\frac{dy}{dt} &= \frac{\beta(1 + \xi v)y}{1 + (1 + \alpha\xi)v} - \delta y
\end{aligned} \tag{20}$$

Using positivity of the states a simple estimate yields,

$$\begin{aligned}
\frac{dv}{dt} &= -v + \frac{1}{\gamma} + \frac{yv^2}{1 + (1 + \alpha\xi)v} \leq -v + \frac{1}{\gamma} + yv, \\
\frac{dy}{dt} &= \frac{\beta(1 + \xi v)y}{1 + (1 + \alpha\xi)v} - \delta y \leq \left(\frac{\beta\xi}{1 + \alpha\xi} + \beta\right)y.
\end{aligned} \tag{21}$$

Note, from (1) a simple comparison with the logistic equation yields, $x < \gamma$, so

$$\frac{1}{x} = v > \frac{1}{\gamma} \implies -v + \frac{1}{\gamma} < 0, \tag{22}$$

inserting this in (21) yields,

$$\begin{aligned}
\frac{dv}{dt} &= -v + \frac{1}{\gamma} + \frac{yv^2}{1 + (1 + \alpha\xi)v} < yv, \\
\frac{dy}{dt} &= \frac{\beta(1 + \xi v)y}{1 + (1 + \alpha\xi)v} - \delta y \leq \left(\frac{\beta\xi}{1 + \alpha\xi} + \beta\right)y.
\end{aligned} \tag{23}$$

By a simple comparison argument $\tilde{v}, \tilde{y}$ are super solutions to v, y, where $\tilde{v}, \tilde{y}$ solve

$$\frac{d\tilde{v}}{dt} = \tilde{y}\tilde{v}, \ \tilde{v}_0 = v_0, \ \frac{d\tilde{y}}{dt} = \left(\frac{\beta\xi}{1 + \alpha\xi} + \beta\right)\tilde{y}, \ \tilde{y}_0 = y_0. \tag{24}$$

Since from (24) $\tilde{y} = y_0 e^{\left(\frac{\beta\xi}{1+\alpha\xi} + \beta\right)t}$, using this in the equation for $\tilde{v}$ yields the following estimate,

$$\tilde{v} \leq C_1 e^{C_2 \left(\frac{\beta\xi}{1+\alpha\xi} + \beta\right)t} \tag{25}$$

where C_1, C_2 can be large constants depending on initial conditions. However, (25) shows $\tilde{v}$ cannot blow up in finite time. By comparison we have

$$v \leq \tilde{v} \leq C_1 e^{C_2 \left(\frac{\beta\xi}{1+\alpha\xi} + \beta\right)t} \tag{26}$$

Thus v also cannot blow up in finite time. This implies $x = \frac{1}{v}$ cannot go extinct in finite time, which is a contradiction to our initial assumption. $\square$

We next prove a technical lemma, required in the proof of Proposition 1.

Lemma 5.1. *Consider the predator-pest system described via (1), and assume we remain in the region of the phase defined by*

$$y \geq x + 1 + \alpha\xi \tag{27}$$

then if the pest is driven to the extinction state, this occurs at the following decay rate

$$x_0 e^{-e^{\left(\frac{\beta\xi}{1+\alpha\xi} + \beta\right)t}} \leq x \leq \frac{x_0 \gamma}{\gamma + x_0 t} \tag{28}$$

Proof. Assume $y \geq x + 1 + \alpha\xi = \frac{1}{v} + 1 + \alpha\xi$, then we have $yv \geq 1 + (1 + \alpha\xi)v$ which implies

$$\begin{aligned}
-v + \frac{1}{\gamma} + \frac{yv^2}{1 + (1 + \alpha\xi)v} &= -v + \frac{1}{\gamma} + \left(\frac{yv}{1 + (1 + \alpha\xi)v}\right)v \\
&> -v + \frac{1}{\gamma} + v = \frac{1}{\gamma},
\end{aligned} \tag{29}$$

inserting the above in (20) yields,

$$\begin{aligned}
\frac{dv}{dt} &= -v + \frac{1}{\gamma} + \frac{yv^2}{1 + (1 + \alpha\xi)v} \geq \frac{1}{\gamma}, \\
\frac{dy}{dt} &= \frac{\beta(1 + \xi v)y}{1 + (1 + \alpha\xi)v} - \delta y \leq \left(\frac{\beta\xi}{1 + \alpha\xi} + \beta\right)y.
\end{aligned} \tag{30}$$

Integrating the above yields,

$$v \geq \frac{t}{\gamma} + v_0 \tag{31}$$

or

$$x \leq \frac{x_0 \gamma}{\gamma + x_0 t} \tag{32}$$

The lower bound follows from the estimate via (26) where

$$\frac{1}{x} = v \leq \tilde{v} < v_0 e^{\left(\frac{\beta\xi}{1+\alpha\xi} + \beta\right)t} \tag{33}$$

thus

$$x_0 e^{-e^{\left(\frac{\beta\xi}{1+\alpha\xi} + \beta\right)t}} \leq x, \tag{34}$$

and the proof is complete. $\square$

Remark 3. The decay rate to the extinction state will depend on the parameter values chosen. There are essentially 2 ways in which pest extinction takes place (Srinivasu et al., 2007; Srinivasu and Prasad, 2010, 2011). The pest can go extinct, and the predator continues to grow exponentially, or it levels off and reaches a steady state. For parameter values such that the predator grows exponentially, the decay in the pest would be closer to super exponential. However, if the predator went to a steady state, the decay would be closer to exponential/polynomial. This is also seen easily in adjusting the condition in Lemma 5.1 to be $yv \geq 2(1 + (1 + \alpha\xi)v)$, which yields, $\frac{dv}{dt} \geq -v + \frac{1}{\gamma} + 2v > v$. Further yielding, $v > v_0 e^t$ or $x < x_0 e^{-t}$.

We next show the proof of Proposition 1.

Proof. We can consider an arbitrarily large quantity of additional food by taking the limit as $\xi \to \infty$ in (34) to yield

$$\lim_{\xi \to \infty} x_0 e^{-e^{\left(\frac{\beta\xi}{1+\alpha\xi} + \beta\right)t}} = x_0 e^{-e^{\left(\frac{\beta}{\alpha} + \beta\right)t}} \leq x. \tag{35}$$

We can consider an arbitrarily high quality of additional food by taking the limit as $\alpha \to 0$ in (34) to yield

$$\lim_{\alpha \to 0} x_0 e^{-e^{\left(\frac{\beta\xi}{1+\alpha\xi} + \beta\right)t}} = x_0 e^{-e^{(\beta\xi + \beta)t}} \leq x. \ \square \tag{36}$$

Remark 4. Notice, v cannot blow up in finite time, even for arbitrarily large ξ. This is easily seen from the form of the exponential in (26), and taking the limit therein as $\xi \to \infty$. Thus even arbitrarily large constant quantities of additional food, cannot drive the pest x to extinction in finite time. The same applies for constant quality. Recall the quality of additional food is $\frac{1}{\alpha}$. Thus in order to increase the quality of the additional food one must decrease α. However, from the form of the exponential in (26), we see that v cannot blow up in finite time, even for arbitrarily small α, or in the limit that $\alpha \to 0$.

We present the proof of Theorem 2.3,

Proof. The following system is derived under the form of f we posit earlier, $f(x, \xi) = x + \xi g(x)$.

$$\frac{dx}{dt} = x(1 - \frac{x}{\gamma}) - \frac{(x + \xi g(x))y}{1 + \alpha\xi + (x + \xi g(x))}, \tag{37}$$

$$\frac{dy}{dt} = \frac{\beta(x + \xi g(x))y}{1 + \alpha\xi + (x + \xi g(x))} + \frac{\beta\xi y}{1 + \alpha\xi + (x + \xi g(x))} - \delta y. \tag{38}$$

WLOG we set $g = \sqrt{x}$, to demonstrate the method of proof.

$$\frac{dx}{dt} = x(1 - \frac{x}{\gamma}) - \frac{(x + \xi\sqrt{x})y}{(1 + \alpha\xi + x + \xi\sqrt{x})},$$
$$\frac{dy}{dt} = \frac{\beta(x + \xi\sqrt{x})y}{(1 + \alpha\xi + x + \xi\sqrt{x})} + \frac{\beta\xi y}{1 + \alpha\xi + x + \xi\sqrt{x}} - \delta y. \tag{39}$$

We also set $v = \frac{1}{x}$, and this yields the following equation for v,

$$\frac{dv}{dt} = -v + \frac{1}{\gamma} + \frac{y(1 + \xi\sqrt{v})v^2}{(1 + \alpha\xi)v + 1 + \xi\sqrt{v}} \tag{40}$$

Our goal is to show that there exist initial conditions s.t. the v solving (45) blows up in finite time.

Note via simple comparison,

$$\frac{dy}{dt} \geq -\delta y \tag{41}$$

Thus $y \geq y_0 e^{-t}$. Note $y \geq 1$ on $[0, \ln(y_0)]$.
Thus inserting this into (45) we obtain,

$$\frac{dv}{dt} = -v + \frac{1}{\gamma} + \frac{y(1 + \xi\sqrt{v})v^2}{(1 + \alpha\xi)v + 1 + \xi\sqrt{v}}$$
$$> -v + \frac{(1 + \xi\sqrt{v})v^2}{(1 + \alpha\xi)v + 1 + \xi\sqrt{v}}, \tag{42}$$

on $[0, \ln(y_0)]$. However, $\tilde{v}$ solving

$$\frac{d\tilde{v}}{dt} = -\tilde{v} + \frac{(1 + \xi\sqrt{\tilde{v}})\tilde{v}^2}{(1 + \alpha\xi)\tilde{v} + 1 + \xi\sqrt{\tilde{v}}}, \quad \tilde{v}_0 = v_0. \tag{43}$$

blows up at a finite time T^*, as long as

$$(1 + \xi\sqrt{v_0})v_0 > (1 + \alpha\xi)v_0 + 1 + \xi\sqrt{v_0}. \tag{44}$$

We only need to choose $v_0 \gg 1$ s.t. $T^* \leq \ln(y_0)$. This completes the proof.

Thus $v \geq \tilde{v}$ by standard comparison and must also blow up in finite time for such sufficiently large initial conditions. Note $v = \frac{1}{x}$, and so large v_0 implies small x_0. This completes the proof. □

We next present the proof of Corollary 1.

Proof. We focus on (37), set $v = \frac{1}{x}$, and follow Theorem 2.3, with $g(x)$ being any general function, to yield

$$\frac{dv}{dt} = -v + \frac{1}{\gamma} + \frac{y(1 + \xi v g(\frac{1}{v}))v^2}{(1 + \alpha\xi)v + 1 + \xi v g(\frac{1}{v})} \tag{45}$$

This will blow up in finite time for sufficiently large initial data v_0 if,

$$\frac{(1 + \xi v g(\frac{1}{v}))v^2}{(1 + \alpha\xi)v + 1 + \xi v g(\frac{1}{v})} > v^q, \quad 1 < q < 2. \tag{46}$$

The finite time blow up of v implies the finite time extinction of x. Simplifying (46) yields the result. The sub linearity requirement on g follows by using a linear/super linear function in (46) to derive a contradiction. □

We next present the proof of Theorem 2.4.

Proof. Via Theorem 2.3 and Corollary 1 we know that there exist initial data for which v solving (45) will blow up in finite time, yielding the finite time extinction of the pest x (see Fig. 3). In order to show that the pest extinction state is globally attracting, it suffices to show blow up will occur for any positive initial condition. To this end it suffices to derive parametric restrictions such that $\frac{dv}{dt} > 0$, implying v will continue to grow. Now once $v \gg 1$, it must blow-up in finite time, via Theorem 2.3 and Corollary 1. Following Theorem 2.3 for $\frac{dv}{dt} > 0$, we require,

$$\frac{1}{\gamma} + \frac{y_0(1 + \xi v_0 g(\frac{1}{v_0}))(v_0)^2}{(1 + \alpha\xi)v_0 + 1 + \xi v_0 g(\frac{1}{v_0})} > v_0 \tag{47}$$

Since for $v_0, y_0 > 0$, $\frac{y_0(1 + \xi v_0 g(\frac{1}{v_0}))(v_0)^2}{(1 + \alpha\xi)v_0 + 1 + \xi v_0 g(\frac{1}{v_0})} > 0$, it suffices to choose $\gamma << 1$, so as to ensure (47) holds. This completes the proof. □

Remark 5. Theorem 2.4 is a stronger result than global asymptotic stability, as the pest free equilibrium is reached in the limit that $t \to T^* < \infty$, and not as $t \to \infty$.

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