Do prey handling predators really matter: Subtle effects of a Crowley-Martin functional response

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ABSTRACT

Predator interference, or a decline in the per predator consumption rate as predator density increases, is generally considered a stabilizing mechanism in two-species predator-prey models. There is significant debate, as to whether prey handling predators, might interfere in the hunting process of prey searching predators, or whether these are mutually exclusive events. In the current manuscript, a three species food chain model, with strong top predator interference is considered. We prove that in terms of explosive instability/finite time blow up, sufficient interference by prey handling predators always tends to *destabilize* the system. The dynamics of a time delayed version, as well as the spatially explicit model are also explored. We use our results to comment on a certain paradox in ecological theory, as well as provide further insight into the nature of predator interference, and exploding populations of invasive species.

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1. Introduction

1.1. Background

Exotic species, commonly referred to as "invasive" species, are defined as any species, capable of propagating into a non-native environment. They are credited with large scale losses to local ecologies and economies [23,41,42,47,48]. Keeping their population in check is thus a paramount issue in ecology. Biological control is a strategy adopted to curtail invasive populations [22,24]. It works on the philosophy of *enemy release*, in which natural enemies of a targeted invasive species, are released against it, in a controlled fashion [22]. An interesting conundrum in the field asks: are generalist predators (those can and do hunt a *variety* of prey) the most *effective* biological control agents? Ecological theory vehemently suggests *no*, primarily due to mutual interference, on the

part of these predators. However, field evidence indicates otherwise [45,46].

In order to investigate this paradox, Parshad et. al in [19], focus on a model for biological control [27], where a generalist top predator [25,26] is released into an ecosystem to control an invasive middle predator, depredating on a prey species. Herein, interactions between the top predator and its target the middle predator, are modeled via a Beddington-DeAngelis functional response, to best mimic the top predator interference [11]. We recap certain ideas of a population *explosion*, as expounded in [19], using standard methods [16,17], via the following connected definitions:

Definition 1.1 (finite time blow-up). Given a mathematical model for a nonlinear process, say through an ordinary differential equation (ODE), one says finite time blow-up occurs if

$$\lim_{t \to T^* < \infty} \|z\|_\infty = \infty,$$

$\|.\|_\infty$ is the standard supremum norm, z is the solution to the ODE in question, and $T^* < \infty$ is the blow-up time. If blow-up does not

occur, that is $T^* = \infty$, we say there is global existence, that is the solution exists for all time.

Definition 1.2 (excessive population of the biological control). Consider a mathematical model (ODE) for the population dynamics of a certain species z, introduced as a biological control. If the model blows-up in finite time, that is

$$\lim_{t \to T^* < \infty} \|z\|_\infty = \infty.$$

then we say that the population z has reached an "excessive" level. In these excessive numbers it is able to wipe out the *target* [15] almost with certainty.

The key idea in [19] then is to equate

blow-up in finite time = control agent being successful

= disaster for ecosystem.

The last equality follows as the control agent (now in excessively large numbers/density) attacks various non targets [15], causing crashes in their populations [47]. In [19], we showed that the interference actually can lead to population explosion. We now break down the interference term *further*. Here we recap certain relevant fundamental notions.

1.2. Interference by handling predators

We begin with a definition

Definition 1.3 (mutual interference). Mutual interference is defined as the behavioral interactions among feeding organisms, that reduce the time that each individual spends in obtaining food, or the amount of food, each individual consumes.

It occurs commonly among predators when prey is scarce, or when the predator population is at high density. The reader is referred to [2–6,30,31] for further details. Note that the classical Holling type II response function, for a population of predators say given by z, depredating on a prey population y, would take the form $f(y) = \frac{y}{y+d}$, with d as a parameter. That is the predator z has a purely prey dependent functional response. Interference is often modeled via the Beddington-DeAngelis response [7] which takes the form $f(y,z) = \frac{y}{y+b_1 z+d}$. The constant b_1 is then the interference parameter, and the response changes due to the assumption that high predator density, should also affect their feeding rate. Intuitively, at higher values of z, $\frac{y}{y+b_1 z+d}$ is small, and the predator feeds less, because there is more time spent as the various predators interfere with each other, in their search for prey [7,30].

Note, the Beddington-DeAngelis formulation assumes that handling and searching are mutually exclusive, that is predators handling prey will *not* interfere with those searching for prey. The Crowley-Martin functional response on the other hand, allows for interference among predators, *even* if they are handling prey [8,21]. It is of the form $f(y,z) = \frac{y}{y+b_1 z+b_2 yz+d}$. The b_2 parameter, in a sense measures the additional interference by prey handling predators [29]. This is extremely realistic in various settings, as a prey handling predator, can easily interfere with a passing predator, in order to say *protect* its prey [28]. There are several other reasons when this occurs in nature [12]. Note there are also several experimental population studies, where the Crowley Martin functional response [8], provides the *best* fit to field data of predators such as wolves *Canis lupus* and Guppies *Poecilia reticulata* [9,28].

Now we delve further into the predator interference term, as modeled via the Crowley-Martin functional response. In essence, we ask

- What is the effect of interference via "handling" predators, on the population dynamics of the three species system considered? We know from [19] that interference can lead to blow

up. However, what if the interference by searching and handling predators is viewed *separately*? What is the role then of additional interference via handling predators?
- What are the connections (if any) of the additional interference, on the paradox of the generalist predator?
- What do these results (if any) foretell, about certain *exploding* populations of invasive species?

1.3. The model system

The model we revisit is one proposed by Jana and Tripathi [1]. Consider a three species food chain model, where a top predator modeled via a modified Leslie-Gower scheme, is introduced into an ecosystem to depredate and thus control an invasive middle predator, that in turn depredates on a prey species. The interaction between middle predator and prey is modeled via a Crowley-Martin type functional response. Various results on the boundedness of solutions to the model, for *any* initial conditions, under certain parametric restrictions are proved. The results of [1] suggest

- Solutions to the model system are globally bounded, under certain parametric restrictions.
- The additional effect of interference by prey handling predators, does *not* cause an effect on the boundedness of solutions.

The model considered in [1] in nondimensionalized form is given by

$$\frac{dx}{dt} = x - x^2 - \frac{xy}{a+x}, \tag{1}$$

$$\frac{dy}{dt} = \frac{\alpha_1 xy}{a_1 + x} - \delta y - \frac{yz}{1 + a_2 y + b_1 z + b_2 yz}, \tag{2}$$

$$\frac{dz}{dt} = cz^2 - \frac{\alpha_3 z^2}{a_3 + y}. \tag{3}$$

with initial conditions

$$x(0) > 0, \ y(0) > 0, \ z(0) > 0. \tag{4}$$

The variable and parameter definitions are given in Table 1:

The model considers interactions between a generalist top predator, specialist middle predator and prey. The interactions between the specialist middle predator and prey are modeled via a modified Holling type II functional response. The interactions between the generalist top predator and specialist middle predator follow a modified Leslie-Gower scheme. That is the generalist top predator grows quadratically, due to sexual reproduction as cz^2, and loses due to intraspecies competition as $-\alpha_3 \frac{z^2}{y+a_3}$. The a_3 signifies that z is a generalist. Also, the middle predator is consumed by the top predator at a Crowley-Martin rate.

Our primary contributions in the current manuscript are:

- We show that the model proposed in [1] can explode/blow-up in finite time, for sufficient initial conditions, even if the parametric restrictions from [1] are met, via Theorem A.1. We quantify this sufficiency condition in terms of the model parameters. This is done via Theorem 2.2.
- We show that the interference by prey handling predators alone, can cause blow-up, whilst there is global existence without this form of interference, via Theorem 2.3.
- We propose a modification to the model proposed in [1], that includes a time delay. The delayed model is shown to possess bounded solutions for *any* initial condition, via Theorem 3.1. The dynamics of the delayed model is also explored numerically, see Fig. 1.