



Original Research Article

Ecoepidemic models with prey group defense and feeding saturation

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ABSTRACT

In this paper we consider a model for the herd behavior of prey, that are subject to attacks by specialist predators. The latter are affected by a transmissible disease. With respect to other recently introduced models of the same nature, we focus here our attention to the possible feeding satiation phenomenon. The system dynamics is thoroughly investigated, to show the occurrence of several types of bifurcations. In addition to the transcritical and Hopf bifurcation that occur commonly in predator–prey system also a zero–Hopf and a global bifurcation occur. The Hopf and the global bifurcation occur only in the disease-free (so purely demographic) system. The latter is a heteroclinic connection for the between saddle equilibrium points where a stable limit cycle is disrupted and where the system disease-free collapses while in a parameter space region the endemic system exists stably.

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1. Introduction

Diseases commonly occur in nature and affect communities. Their role in the shaping the dynamics of populations has been understood since quite some time, with the development of mathematical models for the forecasting of their effects and their possible control. Classical models in this context are the early works on SIRS (Susceptible–Infected–Recovered–Susceptible) models, but during the past century a wealth of other models have been proposed and studied; we mention only the use of the Monod–Haldane function to model the response of individuals to the spread of epidemics, by lowering their contact rates, or models explicitly including viral agents among the systems’ populations, see the review (Hethcote, 2000) for a full account of the field.

Only toward the end of the century epidemic models for populations that vary in time have been introduced, (Busenberg and Driessche van den, 1990; Mena-Lorca and Hethcote, 1992), and this opened up the way for the consideration of disease effects on interacting populations. This has now become an independent field of research, starting from the early papers (Haderl and Freedman, 1989; Beltrami and Carroll, 1994; Venturino, 1994, 1995). More sophisticated models have then been proposed, (Chattopadhyay and Arino, 1999; Haque and Venturino, 2006),

building a field now named ecoepidemiology. For a summary of the first steps into it, see the Part I of (Malchow et al., 2008).

The demographic interactions among populations occupying the same territory have been modeled in various ways, ever since the original investigations of Lotka and Volterra, (Malchow et al., 2008). Other models that are now classical are the Holling–Tanner and Leslie–Gower, (Holling, 1965; Tanner, 1976). In more recent years, the concept of prey group defense has been introduced. Originally, (Freedman and Wolkowicz, 1986), this has been proposed by considerations on possible changes in qualitative properties of the response functions. A recent novel contribution however models the fact that it is the individuals at the edge of the herd that generally suffer the heaviest consequences of the predators’ attacks. Therefore only the subpopulation of individuals that occupy the outermost positions of the flock should be accounted for interactions with predators. Its size is easily identified as being proportional to the perimeter of the area occupied by the herd. This ultimately depends on the square root of the population density, (Ajraldi et al., 2011). The resulting system of differential equations therefore contains a square root term that renders them markedly different from the classical quadratic predator–prey interactions. As a consequence, the dynamics is deeply affected, as this model exhibits limit cycles, which are known to be impossible to arise in the models constructed with bilinear interaction terms. The idea has been further exploited in (Braza, 2012). In the context of predators’ behavior see also related concepts in (Cosner et al., 1999).

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The combination of both the above ideas, namely disease affecting interacting populations and herd behavior, has been explored first in (Venturino, 2011), a study in which the epidemic is assumed to affect the prey, and then in (Belvisi and Venturino, 2013), for the case of diseased predators. In plankton dynamics, this idea has been explored in (Chattopadhyay et al., 2008; Romano et al., 2014), where it is assumed that toxic phytoplankton agglomerates in patches and releases poison through their surface.

Here we want to make a step further, considering also the satiation effect experienced by predators when one type of prey is available in large quantities. After a certain time, the predators disregard the too much abundant food, so that their hunting rate becomes smaller. This phenomenon was firstly modeled in the context of chemical reactions, it is the well-known Michaelis-Menten type dynamics. Later on, in mathematical biology, it has been renamed as Holling type II response function. Here we study this type of situation, combined with the prey gathering together for self-defense purposes. The situation was first proposed in (Gimmelli, 2012) and thoroughly elaborated here, accounting for the epidemics affecting the predators and thereby extending the model (Belvisi and Venturino, 2013). The field evidence of a maximal possible intake of food in a given timespan represents a major reason for proposing this investigation, in that the present model is more adherent to what in fact happens in reality. For drifting herbivores in the savannas, moving in very large herds and subject to individual attacks of predators, the likelihood that they are hunted in the way we describe here is evident. On the other hand, it is well-known also that a large predator after capturing and ingesting a prey, needs some time to digest it, during which the animal remains inactive, from the hunting point of view. A renowned example is provided for instance by the large snakes, after killing a small mammal they remain idle for quite a bit of time, ranging up to a couple of weeks.

The model is analyzed using bifurcation theory (Guckenheimer and Holmes, 1985; Wiggins, 1988, 1990; Kuznetsov, 2004), where the asymptotic behavior of the system (equilibria, periodic cycles, chaos) is evaluated under parameter variation for qualitative changes. A qualitative change in the asymptotic behavior is then referred to as a bifurcation point. For examples of ecological applications in general we refer to (Bazykin, 1998; Kooi, 2003) and references therein. The organizing center of the bifurcation pattern of the model is a point where transcritical, zero-Hopf and Hopf bifurcations intersect. Also a global bifurcation occurs namely a between two saddle equilibrium points. For analysis techniques of this type of heteroclinic connection see (van Voorn et al., 2010).

The paper is organized as follows. We present at first the pure demographic model, since we will need to compare the final results of the ecoepidemic model against its behavior. It is analyzed in Section 2, as on its own it is a new model, differing, as we discussed above, from the classical Holling type II model because it contains the square root term for group defense. It also differs from the herd behavior model presented in (Ajraldi et al., 2011), because it takes into account the feeding satiation phenomenon. In Section 3 we move then to the case of the predators being affected by the disease. In Section 4, the full bifurcation analysis is carried out, completed for the special instance of codimension two bifurcations in Section 5. A final discussion concludes the paper.

2. The interacting population model

We begin with the pure demographic model presentation and analysis, for later comparison purposes. Per se, this is already a new model, extending the basic models considered in (Ajraldi et al., 2011; Belvisi and Venturino, 2013) to the case of feeding satiation coupled with group behavior. There is therefore also an intrinsic interest in its analysis. In broad lines, the ecosystem under

consideration can be described as two populations living in the same environment, each however with different demographic characteristics. In particular the predators behave individually, while the prey instead gather together looking for pastures. Their whole population therefore occupies a contiguous piece of ground. The basic assumption underlying these types of models, (Ajraldi et al., 2011; Belvisi and Venturino, 2013), states that only, or essentially the majority, of the individuals being attacked by the predators will be located at the edge of the territory on which the prey reside. The number of the victims of the attacks will therefore be proportional to the length of a narrow stripe around the boundary of the herd. Since this is essentially a one-dimensional manifold, it is related to the area occupied by the herd via a square root function. The same relationship must therefore hold between the number of individuals suffering attacks at the boundary and the whole prey population. Further, it is widely recognized that an expression of the food intake better than the standard quadratic interactions of the Lotka–Volterra model is represented by the well-known Michaelis–Menten or otherwise called Holling type II response function, in that it sets an upper bound on the possible daily prey consumption. Assuming that the prey reproduce logistically, and that predators are specialists, i.e. they do not have other food sources, and have a bound on the amount of food they can ingest per unit time, which is, as mentioned, expressed via the Holling type II response function, we can describe the interactions as follows

$$\begin{aligned} \frac{d}{dt} \widehat{R}(t) &= r \left(1 - \frac{\widehat{R}(t)}{\widehat{K}} \right) \widehat{R}(t) - \frac{a\sqrt{\widehat{R}(t)}\widehat{F}(t)}{1 + t_h a \sqrt{\widehat{R}(t)}}, \\ \frac{d}{dt} \widehat{F}(t) &= -m\widehat{F}(t) + \frac{ac\sqrt{\widehat{R}(t)}\widehat{F}(t)}{1 + t_h a \sqrt{\widehat{R}(t)}}. \end{aligned} \quad (1)$$

We remove the singularity that arises in the Jacobian when $\widehat{R} = 0$, by setting $\widehat{P} = \sqrt{\widehat{R}} > 0$ thus obtaining

$$\begin{aligned} \frac{d}{d\tau} \widehat{P}(\tau) &= \frac{1}{2} \left[r\widehat{P}(\tau) \left(1 - \frac{\widehat{P}^2(\tau)}{\widehat{K}} \right) - \frac{a\widehat{F}(\tau)}{1 + t_h a \widehat{P}(\tau)} \right], \\ \frac{d}{d\tau} \widehat{F}(\tau) &= -m\widehat{F}(\tau) + \frac{ac\widehat{P}(\tau)\widehat{F}(\tau)}{1 + t_h a \widehat{P}(\tau)}, \end{aligned} \quad (2)$$

which holds for $\widehat{P} > 0$, since in the first equation we have simplified \widehat{P} on both sides. The case $\widehat{P} = 0$ corresponds to setting $\widehat{R} = 0$ into (1) and therefore obtaining that also the predators vanish exponentially fast. The behavior of this purely demographic model has been discussed in depth in (Braza, 2012), especially for the analysis of the equilibrium with vanishing population. The analysis of (Braza, 2012) however makes the simplifying assumption of a HTI model, i.e. setting $t_h = 0$ into (2).

We nondimensionalize it using the following substitutions $P(t) = \alpha\widehat{P}(\tau)$, $F(t) = \beta\widehat{F}(\tau)$, $t = \delta\tau$. We thus find $\frac{d\widehat{P}}{d\tau} = \delta/\alpha dP/dt$, $d\widehat{F}/d\tau = \delta/\beta dF/dt$. Back substitution into (12) gives

$$\begin{aligned} \frac{d}{dt} P(t) &= \frac{1}{2\delta} \left[rP \left(1 - \frac{P^2}{\alpha^2 \widehat{K}} \right) - \frac{\alpha^2}{\beta} \frac{aF}{\alpha + t_h a P} \right], \\ \frac{d}{dt} F(t) &= \frac{F}{\delta} \left[-m + \frac{acP}{\alpha + t_h a P} \right]. \end{aligned} \quad (3)$$

With the choices

$$\beta = \alpha, \quad K = \alpha^2 \widehat{K}, \quad \alpha = t_h a, \quad \delta = \frac{1}{2}, \quad (4)$$

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