



Original Research Article

Effect of a functional response-dependent prey refuge in a predator–prey model

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ABSTRACT

We propose two mathematical models for predator–prey interactions allowing for prey refuge. The novelty lies in the assumption that the amount of prey in refugia is proportional not only to the encounters between prey and predator, but also it is modelled by a Holling type II response function. The second model also accounts for predator's intraspecific competition. We fully analyse the models and discuss all possible coexistence equilibria configurations and their local and global stability. A saddle-node bifurcation analysis is also performed for a wide set of parameter ranges. The ultimate behavior of the systems depends mainly on two relevant parameters, the prey refuge constant and the predator's intraspecific competition.

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1. Introduction

Refuges for the prey have been considered for quite some time. More recently in population dynamics models (Ma et al., 2009a,b; Sarwardi et al., 2012; Sih, 1987; Wang and Wang, 2012). From a theoretical point of view, it has been discovered that including refugia in the ecosystems has generally a stabilising effect on predator–prey interactions (González-Olivares and Ramos-Jiliberto, 2012; Maynard-Smith, 1974), where the refugia are examined in the context of the classical Lotka–Volterra model. More refined refugia models allow for a logistic growth (Turchin, 2003), and in such cases the unique coexistence equilibrium becomes globally asymptotically stable (Collings, 1995; González-Olivares and Ramos-Jiliberto, 2004; González-Olivares and Ramos-Jiliberto, 2003). Also, risky situations that would normally lead to the extinction of the prey may be prevented by the ready availability of places or situations where predation is somewhat lessened. Thus the dynamics of predator–prey systems may be

influenced by the preys use of spatial refuges. This major behavioral trait of prey response to predators' hunting could involve spatial refuges such as burrows or heavy vegetation, that make them less conspicuous to predators. This is easily achievable when environmental heterogeneity favors the discovery of sites that are less accessible for predators (Taylor, 1984), although in general the latter are available only to a given number of prey. Other possible strategies to reduce the risk of being captured are represented by group gathering or simply by reduced movement that diminishes the encounter rates with predators.

All these features allow a fraction of the prey population to defend itself against predators, at least in part (Harrison, 1979; Maynard-Smith, 1974). Denoting by x the prey population and the amount of prey refugia by x_r , so that only $x - x_r$ prey are therefore available for predators' interactions and hunting, several assumptions on the refugia can be made. Indicating with λ a positive constant, it is at first set to a fixed level, $x_r = \lambda$. Alternatively it can be taken to be proportional to the population size, i.e. $x_r = \lambda x$ (González-Olivares and Ramos-Jiliberto, 2012; Harrison, 1979; Maynard-Smith, 1974; Taylor, 1984). Finally it can be assumed to be proportional to the predator density $x_r = \lambda y$ (Ruxton, 1995).

In the case of a constant number of refugia, the dynamical behavior of the neutrally stable Lotka–Volterra model is not

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affected (Maynard-Smith, 1974). However, in a model that in the absence of prey protection shows oscillatory properties, a large refuge replaces the cycles by a stable equilibrium (Hassell, 1978). Refugia in more complex interactions can also induce the presence of a unique stable limit cycle (McNair, 1986). The Lotka–Volterra model including self limitation when the number of refugia is assumed to be proportional to the encounters between prey and predators, i.e. $x_r = \lambda xy$, has been investigated.

In marine reserves, models for “pseudo-refuges” have been considered (Cartigny et al., 2008; González-Olivares and Huincahue-Arcos, 2011; Pezzey et al., 2000). This can be achieved by partitioning the population into two spatially distributed subsets, so that one of them thrives in a protected area, while the other one grows in the open access zone (Dubey et al., 2003).

From all these considerations, it is apparent that the effects of prey refuges on the predator–prey interactions may well be very complicated.

In this paper we present a new model for prey refugia, based on the idea that refugia depend on the encounters between prey and predators. We assume that the interactions between prey and predator are modelled via a Holling type II function. The latter models in general a saturation mechanism, whose meaning here is that the size of the refugia is finite, and the more prey are around, the less they can take cover, until all the refugia are fully occupied. In Section 2 we fully analyse this model, in particular discussing all possible coexistence equilibria configurations.

The second part of the paper, Section 3, contains a slightly more refined model, allowing for predators intra-specific competition. To motivate the extension, we provide an example. In the Sundarban (is the largest single block of tidal halophytic mangrove forest in the world <http://en.wikipedia.org/wiki/Sundarban>) Mangrove ecosystem two fish species coexist, detritivorous fish and their carnivorous fish predators (Ray and Straškraba, 2001). In the major part of the ecosystem, the detritus is abundantly produced. Here the detritivorous fish can find easy protection in the densely flooded bushy parts of the forest. In this area the prey and predators coexist at large population levels. However, observe that there is also a man-reclaimed part of the forest. Here where much anthropogenic stress is felt by the ecosystem, bushes are less available. Consequently, refuge for prey is minimal. The predators can find their prey more easily and therefore compete with each other to capture their food.

2. The basic model

2.1. System setup

We propose and analyze a modified Lotka–Volterra model with self-limitation growth, specifically assuming that the quantity of refugia is proportional to the encounters between prey and predators, the latter being modelled with a Holling type II response function. Let $x(t), y(t)$ stand for the prey and predator populations. To model the amount of refugia x_r available for the prey, we consider a Holling type II response function (Holling, 1965), $\theta x(a+x)^{-1}$, which describes the number of prey escaped against one predator per unit of time. Here θ denotes the prey refuge constant and a is the prey half saturation constant. The Holling type II response function is more apt to describe interactions in large populations. It is given by a hyperbola, rising up to a horizontal asymptote reflecting the maximum rate at which the prey take cover. The Holling type II function in general is used to model the phenomenon of predators satiation, which is experienced when a large population of prey is available. After a while, the too common prey is avoided, the predators preferring a more varied diet, if available. Therefore, the total cover available for the prey can be expressed by the function $x_r = \theta xy(a+x)^{-1}$. On the basis of the above discussion, we consider the following model, assuming that the populations are uniformly

distributed in the environment and disregard other features such as sex or age structure.

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - m\left(1 - \frac{\theta y}{a+x}\right)xy, \tag{1a}$$

$$\frac{dy}{dt} = \left(emx\left(1 - \frac{\theta y}{a+x}\right) - d \right)y. \tag{1b}$$

All the parameters are positive, defined as follows: r, k, m, e, d stand respectively for prey intrinsic growth rate, environment’s carrying capacity, consumption rate, conversion rate, predator death rate.

The first equation contains the prey dynamics, accounting for logistic growth; the interaction term with predators is assumed to be of a mass action type, but it is scaled via a factor accounting for the possibility that some of the prey to take cover when under attack. The latter, as previously mentioned, is taken in the form of a Holling type II term. This very same term reappears in the second equation, containing the predators’ dynamics. In addition, we find another term accounting for their natural mortality.

2.2. Boundedness

By standard simple arguments, one can show that the solution of the system (1) always exists and stays positive, that is the system is dissipative.

From the first equation of (1), we have

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - m\left(x - \frac{\theta xy}{a+x}\right)y < rx\left(1 - \frac{x}{k}\right) < \frac{rx}{k}(k-x). \tag{2}$$

By simple standard arguments we have

$$\limsup_{t \rightarrow +\infty} x(t) < k.$$

Next from the second equation of (1), we have

$$\frac{dy}{dt} = \left(em\left(x - \frac{\theta xy}{a+x}\right) - d \right)y < em\left(\frac{ax+x^2 - \theta xy}{a+x}\right)y, \tag{3}$$

so it follows that

$$\limsup_{t \rightarrow +\infty} y(t) < \frac{a+k}{\theta}.$$

Hence the system is dissipative. Now there exists a $T > 0$ such that for all $t > T$, we have $x(t) < k + \epsilon =: W$ and $y(t) < \frac{a+k}{\theta} + \epsilon =: W_1$.

Proposition 2.1.

- (a) All the solutions of system (1) which initiate in R_+^2 are uniformly bounded.
- (b) The following is an invariant compact set

$$\Sigma = \left\{ (x, y) \in R_+^2 : 0 \leq x \leq k, 0 \leq y \leq \frac{a+k}{\theta} \right\}.$$

Proof.

- (a) Define the environment’s total population $\pi = x + y$. For a suitable $d > \mu > 0$, the following inequalities hold, since $0 < e < 1$

$$\begin{aligned} \frac{d\pi}{dt} + \mu\pi &= rx\left(1 - \frac{x}{k}\right) - m\left(x - \frac{\theta xy}{a+x}\right)y + \left(em\left(x - \frac{\theta xy}{a+x}\right) - d \right)y + \mu\pi \\ &\leq x\left(\mu + r\left(1 - \frac{x}{k}\right)\right) - (d - \mu)y - mxy(1 - e) + \frac{m\theta xy}{a+x}(1 - e), \\ &\leq k\frac{(\mu + r)^2}{4r} + m\theta W_1(1 - e) =: \phi. \end{aligned}$$

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