



The effect of state dependent delay and harvesting on a stage-structured predator–prey model



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ABSTRACT

We propose and analyze a stage-structured predator–prey model in which the time from birth to maturity is directly related to the number of individuals present. Individuals mature more quickly when there are fewer of them around. The state dependent time delay is taken to be an increasing differentiable bounded function. In this research, we study the dynamics of our model analytically. We present results on positivity and boundedness of all populations. Criteria for the existence of all equilibria and uniqueness of a positive equilibrium are given. In order to observe the effect of state-dependent maturation delay, local stability analysis around all equilibria of the proposed model is discussed due to variation of maturation delay. Also, global stability of trivial and the boundary equilibria is investigated, using Liapunov functional and LaSalle invariant principle. To investigate the effect of state-dependent maturation delay and the harvesting effort of all species we carried out numerical simulations.

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1. Introduction

Predator–prey interactions have remained an important area in theoretical ecology since the famous Lotka–Volterra equation. It is assumed in these models that each individual predator admits the same ability to attack prey. This assumption is obviously unrealistic for many populations. In ecology, realistic models often need to incorporate a time lag between the moment an action takes place and the moment its effect is observed, that is, a real system should include an extra term which is called the time delay. In the natural world, many population species go through two or more life stages as they proceed from birth to death.

Most of the models in the literature always assumed that all individuals of a single species have largely similar capabilities to hunt or reproduce. However, the life cycle of most, if not all, animals and insects consists of at least two stages, immature and mature. Therefore, it is practical to introduce the stage structure into the competitive or predator–prey models. Stage-structured models have received much attention in recent years. These kinds of models are appropriate for many species in the real world, such as mammalian populations and some amphibious animals. The pioneering work of Aiello and Freedman [1] on a single species stage-structured model represents a mathematically careful and ecologically meaningful model formulation approach. They considered various aspects of their model including positivity and boundedness of solutions. They also established that all ecologically relevant solutions tend to the positive equilibrium solution.

It is well known that harvesting has a strong impact on the dynamic evolution of a population; there has been considerable interest in the modeling of harvesting of biological resources. In recent years, there has been growing interest in the study of a stage-structured predator–prey systems with harvesting. Following the way of Aiello and Freedman, many authors studied

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different kinds of stage-structured models with and without harvesting (see, for example [2–9]). A good overview on stage-structured models can be found in the book by Murdoch et al. [10].

Although the appearance of state-dependent delays in the literature goes back to the 19th century, the study of them has recently been re-activated due to their frequent occurrence in a wide variety of situations. Introducing a state-dependent delay in modeling real phenomena results frequently from an attempt to account for the influence of some facts on the behavior of a population. Nevertheless, it is difficult to evaluate the actual impact of a state-dependent delay on the response of the model, in particular in what concerns the instability due to oscillations. In fact, these models pose problems even with regard to the resolution and uniqueness of solutions. Following, Aiello and Freedman [1], Aiello et al. [11] modified their stage-structured population model [1] to include a state-dependent time delay based on the biological backgrounds on the Antarctic whale and seal populations. It was observed by Gambell [12] that the length of time to maturity is a function of the amount of food available. For example, in the case of Antarctic whale and seal populations, before World War II, due to the large amount of whales, small whales took seven to ten years, and large whale species took 12–15 years to reach maturity. But after the introduction of factory ships after the war, and a consequent depletion of the large whale populations, there was an increase in the krill available for the seals and the remaining whales. It was then noted that seals took only three to four years to mature and small whales now only took five years. Maturation time for large whales also significantly decreased.

Therefore, in [11] they include a monotonically increasing, state-dependent time delay instead of a constant time delay. The existence of such monotonically increasing time to maturity has been observed in other contexts as well. For example, Birth and Andrewartha [13] describe how the duration of larval development of flies is a nonlinear increasing function of larval density. The precise model of Aiello et al. [11] is

$$\begin{aligned} u_i'(t) &= \alpha u_m(t) - \gamma u_i(t) - \alpha e^{-\gamma \tau(z)} u_m(t - \tau(z)), \\ u_m'(t) &= \alpha e^{-\gamma \tau(z)} u_m(t - \tau(z)) - \beta u_m^2(t), \end{aligned}$$

where $z = u_i + u_m$ and $0 < \tau_m \leq \tau(z) \leq \tau_M$ with $\tau(0) = \tau_m$ and $\tau(\infty) = \tau_M$. They found that there always exists a positive equilibrium, and they obtained criteria for uniqueness as well as local asymptotic stability. Also they obtained bounds for the eventual behavior of $u_i(t)$ and $u_m(t)$.

Recently, Al-Omari and Gourley [14], derived and studied a stage-dependent population model with state-dependent time delay where the immature birth rate is taken to be a general function of the mature population around and the death rate for the mature is linear. The state-dependent time delay is taken to be an increasing differentiable bounded function of the total population (mature and immature). The model takes on the following form:

$$\begin{aligned} u_i'(t) &= R(u_m(t)) - \gamma u_i(t) - e^{-\gamma \tau(u)} R(u_m(t - \tau(u))), \\ u_m'(t) &= e^{-\gamma \tau(u)} R(u_m(t - \tau(u))) - d u_m(t), \end{aligned}$$

where the function $R(u_m(t))$ behaves linearly in u_m for small u_m , but is effectively zero for large u_m . The function $R(u_m)$ represents the birth rate, and the two terms $-\gamma u_i$ and $-d u_m$ represent the deaths of immatures and matures respectively. The delayed term in both equations represents adult recruitment. They proved that the solution of the mature equation is always positive and that the solution of the mature and immature equations are bounded above. The positivity of the solution of the immature population has been established under some additional conditions. They investigated the possibility for a non-trivial equilibrium to exist. They proved that the zero equilibrium is globally asymptotically stable in the situation when the positive equilibrium does not exist. The positive equilibrium is asymptotically stable in the situation when it is close to the zero equilibrium. Recently, few progress in the literature has been made in this direction (see, for example [15–18]).

In view of such stage-structured predator–prey model, Gourley and Kuang [19] formulated a general and robust predator–prey model with stage-structure with constant maturation time delay and performed a systematic mathematical and computational study. They have shown that there is a window in maturation time delay parameter that generates sustainable oscillatory dynamics.

$$\begin{aligned} x'(t) &= rx(t) \left(1 - \frac{x(t)}{k} \right) - ay(t)P(x(t)), \\ y'(t) &= be^{-\gamma \tau} y(t - \tau)P(x(t - \tau)) - dy(t), \\ y_j'(t) &= by(t)P(x(t)) - be^{-\gamma \tau} y(t - \tau)P(x(t - \tau)) - \gamma y_j(t), \end{aligned} \quad (1.1)$$

where $x(t)$ and $y(t)$ represent prey and mature predator densities, respectively. $y_j(t)$ denotes the immature or juvenile predator density. Here r is the specific growth rate of the prey and k is its carrying capacity. The parameters b and d are the adult predators' birth and death rates, respectively. In addition, the juveniles suffer a mortality rate of γ (the through-stage death rate) and take τ units of time to mature. The function $p(x)$ is the adult predators' functional response and it is assumed to be differentiable and satisfies $P(0) = 0$ and $P(x)/x$ bounded for all $x \geq 0$.

2. Model formulation

Motivated by the above works, the objective of this paper, is to adapt and study system (1.1) by introducing stage-structured predator prey population model with a state-dependent time delay and harvesting. And for the sake of simple, we consider the

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