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# Biological mechanisms of coexistence for a family of age structured population models



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HIGHLIGHTS

- We construct a family of predator-prey models with age structure in both species.
- We introduce biological mechanisms in the models to achieve coexistence.
- Factors of intraspecific competition, selective predation and cannibalism among predators are included.
- Numerical and analytical parametric studies of the models are carried out.

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#### 1. Introduction

#### ABSTRACT

In this work we construct a family of age structured predator-prey models in order to introduce different mechanisms of biological interest that lead us to infer conditions where coexistence among both species may be possible. We analyze the relationship of existence of stable solutions, mathematical equivalent to coexistence, with biological mechanisms such as intraspecific competition, selective predation and cannibalism among predators. © 2018 Elsevier B.V. All rights reserved.

One of the common assumptions used in basic population models is the homogeneity of individuals, which means that individuals with different characteristics like age, height or sex, in a particular population are represented by a single state variable. Such models implicitly assume that the birth rate of young and mature individuals is the same. It is also assumed that the offsprings of predators have the ability to hunt for prey immediately after birth. However, in real situations most species undergo several developmental stages throughout his life. Thus, the reproduction, survival and predation rates are different for each one of such stages. Therefore, in order to simulate realistically population dynamics is important to include diverse structures in the models.

Structured models describe the distribution of individuals through different classes or categories [1,2]. The definition of these classes is based on individual differences that may affect important processes such as reproduction, death, nutrition, among others. For example, categorizing individuals can be based on their age, size, gender, spatial localization, genetic differences, behavioral activities, etc. These models describe the dynamics of class distributions of the population and as a result the dynamics of the population as a whole. To cite just a few examples: structured models are required for the study of problems related to the effects of maturation and delay gestation [3]; intra-class competition between large and small individuals or between juveniles and adults [4]; intraspecific predation (cannibalism) [5–8]; scenarios where individuals

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are subject to strong competition or predation before reaching reproductive maturity [9]; selective predation on prey of certain ages and/or sizes [10–12].

An equation for the modeling of a single population with age structure was first proposed about a century ago by A. McKendrick [13] who pioneered the use of mathematical methods in epidemiology. Such theory was generalized to include nonlinear effects by Gurtin and MacCamy [14]. Some years later, Levine [15] combined age structured McKendrick models with the predator–prey models of Lotka–Volterra and Kolmogorov type to study the effects of different patterns of selective predation. One of the conclusions was that if predators feed only on prey of certain age range, the resulting system becomes unstable with oscillations of unbounded amplitude.

Generally, unstable solutions arise when the proposed model fails to incorporate important saturation terms. Recently, Solis [8,16–18] proposed different biological mechanisms, like fishing on predators and prey intraspecific competition, in order to stabilize Levine's system. These works, in addition to many others that can be found in the references, show that structured models can display very interesting and complicated dynamic behavior. It is important to emphasize that the introduction of a structure, age for example, complicates technically the analysis of the models. For this reason, it is common to assume that such structure only affects one species. However, in this work we have several goals in such regard. The first one is to generalize some existing predator–prey models in the literature by considering age structure in both species. The inclusion of age structure only on the prey has been analyzed in [16]. It was believed that including age structure only on the predators will give a similar model with the same dynamical characteristics as the previous one. Showing that actually a different model arises is the second goal of this work. The final goal is to analyze different biological mechanisms in order to obtain coexistence on the age structured models.

This paper is organized as follows: In Section 2, we derived a family of base predator–prey models with age structure in both species. Such models will be based essentially on a pair of McKendrick equations for the densities of the two species. In Section 3, we introduce biological mechanisms such as intraspecific competition and selective predation in order to obtain coexistence in both species. In Section 4, we introduce a mechanism of intraspecific predation known as cannibalism. Analytical and numerical bifurcation analysis will be carry out in both previous sections for the purpose of identify parameter values for which the models have stable equilibria and/or stable periodic solutions which are the mathematical equivalent to coexistence. The general conclusions of the work are summarized in Section 5.

#### 2. Structured base model

Let  $\rho(\omega, t)$  and  $\sigma(\omega, t)$  be nonnegative functions denoting the number of prey and predators at time *t* of age  $\omega$ , respectively. The total population of prey and predators are given by

$$P(t) = \int_0^\infty \rho(\omega, t) d\omega, \qquad D(t) = \int_0^\infty \sigma(\omega, t) d\omega.$$

We assume that the mortality functions, denoted by  $\mu$  and  $\nu$ , depend<sup>1</sup> not only on the biological or evolutionary processes inherent of their own species seen as a isolated ecosystem but also on their interacting species. Considering a McKendrick type of evolution for both densities we obtain:

$$\frac{\partial \rho}{\partial \omega} + \frac{\partial \rho}{\partial t} + \mu(\omega, P, D)\rho = 0,$$
  
$$\frac{\partial \sigma}{\partial \omega} + \frac{\partial \sigma}{\partial t} + \nu(\omega, P, D)\sigma = 0.$$

.....

Let us assume that the process of birth in both populations (or the entry of zero-age individuals) is governed by the following equations:

$$B_{\rho}(t) = \int_{0}^{\infty} \beta_{\rho}(\omega)\rho(\omega, t)d\omega, \tag{1}$$
$$B_{\sigma}(t) = \int_{0}^{\infty} \beta_{\sigma}(\omega)\sigma(\omega, t)d\omega, \tag{2}$$

where the fertility functions  $\beta_{\rho}$  and  $\beta_{\sigma}$  are nonnegative functions of age modeling the capability of procreation of individuals of age  $\omega$ . Expressions (1)–(2) represent the birth rates for prey and predators respectively. We select functions of the form:

$$\beta_{\rho}(\omega) = \beta_1 \omega e^{-c\omega}, \quad \beta_{\sigma}(\omega) = \beta_2 \omega e^{-k\omega}$$

Notice that in mathematical terms, they are nonnegative functions, bounded and reaching a maximum at a relatively young age and then decreasing monotonically to zero. In order to obtain a system of equations for both total populations we make use of the following proposition taken from [4]:

<sup>&</sup>lt;sup>1</sup> Later on, we will also assume the dependence of the predator mortality on the renewal function.

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