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Continuous-time, stage-structured, multiple-species model with applications to amphibians ☆

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A R T I C L E I N F O

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A B S T R A C T

Since the 1980s, biologists have noticed a major decline in amphibian population. The reason this is so alarming is because amphibians have been seen as a "Canary in the mine" when it comes to the world's environmental changes. With global warming and CO_2 emissions all over the news, we have become more aware of how we are impacting our world. If the decline of amphibians is a precursor to what is happening with the environment, then we need to find a good model to give us estimates on what is going to happen in the future. Here we used a predator–prey-competition model to help investigate how three amphibians might interact when confined to the same area.

1. Introduction

Recently, amphibians have been declining worldwide. [6,10,16,22]. There are many hypotheses about why this decline is occurring including viruses, disease, habitat destruction, introduction of new predators, etc. [2,3,5–9,11,16–19,21,25,26]. In this paper, we assume that there are three types of amphibians interacting within the same area, toads, frogs, and salamanders.

We chose to use a modified Lotka–Volterra model with competition amongst the prey and density dependence amongst all animals to model limited resources. Of course such models are not perfect as they can easily contradict observed population levels amongst predators and prey [13,29]. For a summary of common predator–prey models, the interested reader can turn to [4]. For an introduction to the analysis of several basic predator–prey models, see [1,23,12].

The basic model Lotka–Volterra, constructed independently in 1925 and 1928 by Lotka [20] and Volterra [28], respectively, is a predator–prey model where the predator, P, dies exponentially in the absence of its prey, N, and the prey grows exponentially in the absence of the predator. The basic predator–prey model is the system of differential equations

$$\frac{dN}{dt} = aN - bNP, \quad \frac{dP}{dt} = cNP - dP.$$

The predation term, bNP, and gain from predation, cNP, is based upon the concept of mass action. Growth of prey is modeled by aN and death of the predators by dP. This model exhibits a classic oscillatory behavior with the rise and fall in the number of predators slightly behind that of the prey. That is, when prey is abundant, this causes the number of predators to increase. However, with an increase of predators, consumption of prey increases, driving the number of prey down. This decrease in prey eventually forces a decrease in predators, which in turn allows prey to again increase, starting the cycle over again. These ideas have been generalized to any number of predator and prey species [23].

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Of course, exponential growth of prey in the absence of predators is not very realistic. So, models often include density dependence to simulate bounds on resources or simulate how hard it is for predators to hunt prey. A common assumption is to assume logistic growth on the prey with some maximum carrying capacity. Often the predation term is also modified to simulate different hunting strategies that a particular predator might exhibit. A predator's survival could be modified based upon certain characteristics it shows. See, for example [15,24].

A common competition model [1,12,23], is the following

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12}\frac{N_2}{K_1}\right), \quad \frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21}\frac{N_1}{K_2}\right).$$

All parameters are assumed positive. In this model, N_1 grows logistically if its competitor N_2 is not present. However, when both species are present, then the term b_{12} measures the negative effects that species N_2 has upon N_1. Of course, similar statements hold for N_2. Considering the possible equilibria, we see that there are four cases to consider. $(K_1, 0)$ is locally asymptotically stable, $(0, K_2)$ is locally asymptotically stable, both $(K_1, 0)$ and $(0, K_2)$ are locally asymptotically stable, or the positive equilibrium is locally asymptotically stable.

However, none of these basic models capture exactly what we wish to model. We wished to construct a predator–prey model where the prey competed amongst themselves for resources, the predators could survive without the prey, and all three species were limited in growth by finite resources. A much more general model can be defined for multispecies interactions, see for example [14]. This model has the form

$$\frac{dN_i}{dt} = N_i\left(b_i + \sum_{i=1}^{m} a_{ij} N_j\right), \quad i = 1, 2, \ldots, m. \tag{1.1}$$

We use a specific instance of this model in this paper.

2. The model

We choose to model adult animals and denote salamanders with an A, toads by $\widetilde{A}$, and frogs by $\widehat{A}$. This naming convention holds for virtually all parameters in the model, with the exception of predation terms in the salamander equation. Since all the species are living around one lake or pond then the equations need to also have interaction terms. To simulate competition, predation, and cannibalism, the death rate is assumed to be a function of the total animals. We assume that salamanders eat both frogs and toads and other, smaller creatures, living in and around the lake. Thus salamanders do not depend solely upon toads and frogs for their survival. Hence, we include terms to simulate the predation of frogs and toads by salamanders. We also assume that frogs and toads compete for resources. The terms with P and ϕ indicate negative effects from predation and competition terms, respectively. The terms with a δ indicate self competition or density dependence. The terms with a ρ indicate positive effects due to predation. For example, the rate of change of salamanders is given by $GA - \delta A^2 + \hat{\rho} A\widehat{A} + \tilde{\rho} A\widetilde{A}$ where GA represents the recruitment of adults, δA^2 the negative effect of salamander density dependence, and $\hat{\rho} A\widehat{A}$ and $\tilde{\rho} A\widetilde{A}$ the gain by predation on frogs and toads, respectively. Fig. 1 is a compartmental diagram describing our model. Expressions beneath an arrow indicate a loss to a compartment while expressions above an arrow represent a gain. For example, the term $\tilde{\rho} A\widetilde{A}$ represents a gain to A due to predation while $\widetilde{P} A\widetilde{A}$ represents the loss to $\widetilde{A}$ due to predation. Model (2.1) is given by

$$\begin{aligned}
\frac{dA}{dt} &= GA - \delta A^2 + \hat{\rho} A\widehat{A} + \tilde{\rho} A\widetilde{A},\\
\frac{d\widetilde{A}}{dt} &= \widetilde{G}\widetilde{A} - \tilde{\delta}\widetilde{A}^2 - \widetilde{P}\widetilde{A}A - \tilde{\phi}\widetilde{A}\widehat{A},\\
\frac{d\widehat{A}}{dt} &= \widehat{G}\widehat{A} - \hat{\delta}\widehat{A}^2 - \widehat{P}\widehat{A}A - \hat{\phi}\widehat{A}\widetilde{A}.
\end{aligned} \tag{2.1}$$

The biological meaning of the parameters is included in Table 1.

2.1. Equilibria

We first consider the various equilibria. Stability of selected equilibria will be investigated in the next section. Clearly, extinction is one equilibrium. If we assume that two of the three animals die out, then the resulting system collapses to a single differential equation. For example, if salamanders survive while toad and frogs become extinct,

$$\frac{dA}{dt} = GA - \delta A^2.$$

This has a well known positive equilibrium $\mathcal{A} = \frac{G}{\delta}$ which is a ratio of the recruitment rate to the removal rate of adult animals. The other two are similar.

Now, we consider the case where two species survive. Note that due to symmetry contained within the model, we need only consider the cases where salamanders and either frogs or toads survive, and the case where salamanders do not survive. Thus, when salamanders and toads survive, Model (2.1) reduces to Model (2.2)