



Original Research Article

Multiple stable states in a model based on predator-induced defenses



Eduardo González-Olivares^{a,*}, Betsabé González-Yañez^a, Ruth Becerra-Klix^b,
Rodrigo Ramos-Jiliberto^{c,d}

^a Pontificia Universidad Católica de Valparaíso, Av. Brasil, 2950 Valparaíso, Chile

^b Facultad de Ingeniería y Ciencias, Universidad Adolfo Ibáñez, Av. Padre Hurtado, 750 Viña del Mar, Chile

^c Centro Nacional del Medio Ambiente, Universidad de Chile, Av. Alcalde Fernando Castillo Velasco, 9975 La Reina, Chile

^d Programas de Postgrado, Facultad de Ciencias, Pontificia Universidad Católica de Valparaíso, Av. Brasil, 2950 Valparaíso, Chile

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ABSTRACT

A large variety of antipredator defenses are exhibited by plants, animals and microbes in nature. A deep understanding of the dynamic consequences of prey responses to predation risk is essential for building a comprehensive theory of food webs. Here we present a simple classification of prey defenses based on the sensitivity of prey immunity to predation respect to abundances of prey and predators. Only three out of six defense types have been analytically studied in the context of predator–prey dynamics, which reveals a serious gap in our current knowledge of ecological interactions. In this study we present a mathematical analysis on a widely occurring type of prey defense whose behavior has not been established in exact terms. The study model considers prey whose average immunity to predators is enhanced by predator abundance. This case, known as inducible defenses, has been reported for a wide array of species. Our results reveal a rich dynamic behavior, in which the predator–prey system exhibits either one, two or three positive equilibrium points, with up to two attractors. Thus, inducible defenses constitute a mechanism that could drive alternative stable states even in very simple food web models.

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1. Introduction

One of the most relevant features determining the dynamics of ecological food webs is the ability of prey to avoid being killed by their predators (Fryxell and Lundberg, 1997; Kondoh, 2007). Antipredator defenses prevent prey losses as well as predator feeding, thus affecting the transfer of energy and matter through trophic paths. Moreover, empirical and theoretical studies have shown that the expression of antipredator defenses may exert strong influences on the long-term stability of populations and communities (Matsuda et al., 1996; Bolker et al., 2003; Krivan and Sirotnik, 2004; Ramos-Jiliberto, 2003; Vos et al., 2004).

The analysis of mathematical models has been crucial for the development of ecological knowledge and food web theory in particular. Early theoretical studies on antipredator defenses focused on understanding the dynamical consequences of the use of physical refuges by prey. Simple physical refuges have a fixed

capacity to protect a number of prey, independent on actual prey population size (McNair, 1986). Another reasonably well studied form of prey defenses consists of the suppression, by a given fixed amount, of the average vulnerability of prey to being killed by their predators (González-Olivares and Ramos-Jiliberto, 2003). These prey attributes are termed constitutive defenses, and include any trait that may impede encounters with and successful attacks from predators. In addition, a different kind of defensive traits involves the density-dependent temporal suppression of prey vulnerability to predation (Tollrian and Harvell, 1999). This type of defenses, often called inducible defenses, are phenotypic prey responses to variations in population size of their predators, but can also be modulated by prey density (Tollrian et al., 2015). The underlying mechanisms by which prey exhibit some kind of immunity to predators are diverse, such as development of spines, chemicals, special color patterns, behavioral avoidance, hiding, shifts in life-history traits, among many others.

Predator–prey theory has been at the core of modern ecological knowledge and has exhibited notable developments (Berryman, 1992; Abrams, 2000) during the last decades. However, to gain a deeper understanding of the collective behavior of communities, ecosystems, and particularly food webs, we require building a

* Corresponding author.

E-mail addresses: ejgonzal@ucv.cl (E. González-Olivares), ruth.becerra@uai.cl (R. Becerra-Klix), ramos.jiliberto@gmail.com (R. Ramos-Jiliberto).

comprehensive theory of predator–prey interactions that should incorporate a rigorous understanding of prey responses to predation risk. A major challenge toward this goal is to address the wide variety of behavioral, morphological and life-historical defenses, either constitutive or inducible, observed in nature, which are known to exert specific effects on food web stability (Ramos-Jiliberto et al., 2007).

In order to classify the different forms of prey defenses into few manageable types, consider the conceptual model shown in Fig. 1. This idealized picture includes consumptive and non-consumptive effects of predators. We root this model in that prey exhibit some trait T_x which determines their immunity to predators. Examples of such traits include thickness of shells or covers, body transparency, spine length, concentration of chemical compounds, hiding or avoidance behaviors, among others. For modeling purposes, we consider trophic interactions governed by the biomass conversion principle (Ramos-Jiliberto, 2005) and thus modeled by Gause-type equations (Freedman, 1980). A family of simple food chain models that satisfy our assumptions is:

$$\frac{dn_i}{dt} = [\varepsilon_i F_i(n_{i-1}, T_{i-1}, T_i) - b_i n_i] n_i - F_{i+1}(n_i, T_i, T_{i+1}) n_{i+1} \quad (1)$$

where n_i is the population size of a species of trophic level i , parameter ε_i represents conversion efficiency of food into population biomass and b_i is a self interference coefficient due to intraspecific competition for fixed resources. Functions F_i are the functional responses of predators of trophic level i , which depend on the density of prey of trophic level $i - 1$, and the expression of defensive traits T_i in both prey and predators. Defensive traits of prey lead to decreasing their own mortality rate due to predation, whereas defensive traits of predators lead to decreasing their feeding rates on prey due to non-consumptive effects exerted by upper predators. Hereafter we further assume that non-consumptive effects of predation, and therefore fitness costs of defenses, are negligible and that functional responses are linear respect to prey availability.

In addition, we consider that the defensive trait set T_x determines the immunity of prey to predation, defined here as $R = x_r/x$, where x_r represents the prey biomass that is immune to predation and x is total prey population biomass. Thus, prey availability to predators is represented by $x(1 - R)$. A one-prey-one-predator system derived from (1) satisfying the above assumptions reduces to

$$\begin{aligned} \frac{dx}{dt} &= r \left(1 - \frac{x}{K}\right) x - qx(1 - R)y \\ \frac{dy}{dt} &= (px(1 - R) - c)y \end{aligned} \quad (2)$$

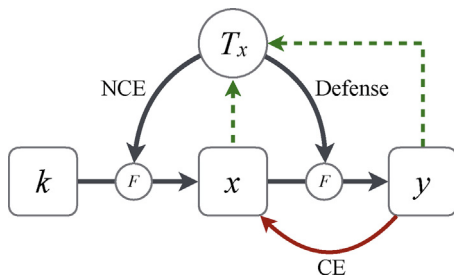


Fig. 1. Conceptual model of prey defenses. Predators of abundance y consume prey of abundance x which in turn consume resources of abundance k . Consumption rate is governed by functional responses F . Prey x exhibit some set of traits T_x which suppresses predator's functional response F and consumptive effects (CE). In addition, the defensive traits exert some non-consumptive effects (NCE), usually a reduction in prey's functional response. Trait expression could be triggered by an increase in either predator abundance, prey abundance or both (dashed lines).

where $x = x(t)$ and $y = y(t)$ indicate prey and predator population size (in biomass units), with $\mu = (r, K, \delta, q, p, c) \in \mathbb{R}_+^6$. The parameters have the following biological meanings: r is the intrinsic per capita prey growth rate, K is the prey carrying capacity, q is the per capita predator consumption rate, p is the efficiency at which predators convert consumed prey into new predator biomass and c is the natural death rate of predators. Prey population grows according to the logistic model in the absence of predation, and it is killed at a rate proportional to the product of prey availability and predator biomass abundance. Predator population gains biomass from prey consumption and decays at a constant per capita natural rate. However, antipredator defenses differ qualitatively in the mechanisms that trigger the expression of defensive traits T_x and determine prey immunity R (Table 1). We propose a classification of prey defenses into six basic types, according to the sensitivity of R to prey and predator densities. Here we assume that R should not decrease with predator abundance y , to be considered an antipredator response. All other cases are included in Table 1. A contemporary theory of food webs should consider qualitative results established by the analytical study of this variety of antipredator prey responses, at least included in the most simple predator-prey models such as (2). As shown in the last column of Table 1, to our knowledge half of the basic types of antipredator defenses has not been yet analytically studied even within the most simple predation models. This reveals a serious gap in our current knowledge of ecological interactions. In this study we contribute to fill this gap, by studying mathematically the dynamical consequences of a simple predator-prey model of the type of (2) and including the triggering mechanism $R = \delta y$.

2. The model

In this study we analyze model (2) assuming $R = \delta y$. The study system is represented by the following ordinary differential equations that belong to the classes of Kolmogorov-type and Gause-type models (Freedman, 1980).

$$X_\mu : \begin{cases} \frac{dx}{dt} = r \left(1 - \frac{x}{K}\right) x - qx(1 - \delta y)y \\ \frac{dy}{dt} = (px(1 - \delta y) - c)y \end{cases} \quad (3)$$

Here, we assume that the immunity to predators of an average prey, R , is proportional to predator biomass abundance y , i.e. $R = \delta y$, with $\delta \geq 0$ and $1 - \delta y > 0$. The assumption that immunity to predators increases with predator biomass has been supported by numerous empirical studies (Tollrian and Harvell, 1999). This kind of defensive responses corresponds to what has been called inducible defenses, and the study of their population dynamics consequences in realistic biological scenarios has been carried out using mainly numerical tools (Ramos-Jiliberto, 2003). The lack of previous analytical studies on this type of defenses and their recognized importance in shaping the ecological and evolutionary dynamics of populations (Tollrian and Harvell, 1999) motivates conducting this research. System (3) or vector field X_μ is defined at

$$\Omega = \{(x, y) \in \mathbb{R}_0^2 \mid x \geq 0, y \geq 0\} = \mathbb{R}_0^+ \times \mathbb{R}_0^+, \quad (4)$$

The equilibrium points are $P_0 = (0, 0)$, $P_K = (K, 0)$ and $P_e = (x_e, y_e)$, with $y_e = \frac{px}{cq} \left(1 - \frac{x_e}{K}\right)$, where x_e is solution of a third degree polynomial equation. The equilibrium P_e lies in Ω , if and only if, $x_e < K$.

With $\delta = 0$, the equilibrium points of system (3) are $(0, 0)$, $(K, 0)$ and the unique equilibrium point at the interior of the first quadrant $P_e = \left(\frac{c}{p}, \frac{r(pK-c)}{qpK}\right)$. Constructing a Lyapunov function (Goh, 1980) it can be proved that the point P_e is globally asymptotically stable, if and only if, $c < pK$. Moreover, the point $(K, 0)$ is globally

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