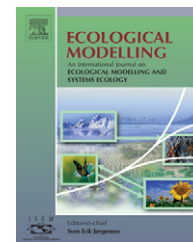


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Pre-encounter versus post-encounter inducible defenses in predator–prey model systems

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ABSTRACT

It has been reported that, in order to reduce mortality, prey are able to change their phenotype in response to cues released from predators. These short-time responses constitute effective antipredator strategies in variable environments, and involve changes in morphology, behavior, physiology or life-history traits of prey individuals belonging to a wide spectrum of taxa. Defenses can be classified into pre-encounter and post-encounter, depending on the phase of the predation process in which they take place. Also, inducible defenses should be costly.

Despite the current knowledge of inducible defenses at the individual level, our understanding of their dynamic consequences at the population and community level is limited. In this work we construct and analyze numerically a predator–prey system, parameterized from published experimental data, in which prey exhibit inducible defenses of the type pre-encounter (affecting attack rate) or post-encounter (affecting handling time) and entailing either metabolic or feeding costs. The above assumptions were analyzed over a gradient of resource availability.

Our results indicated that both types of cost have a similar effect on the dynamics of the model system, but we expect that different costs will produce different outcomes in a more complex model community. Conversely, pre-encounter and post-encounter IDs define domains of attraction with different size and shape within the studied sections of the multi-dimensional parameter space. Roughly speaking, post-encounter IDs determine a more rich dynamics when plausible parameter values are chosen, and the effect of resource density is different if the ID is handling-time based or attack-rate based. In agreement with previous works, our analyses indicate that IDs can damp population oscillations and prevent the paradox of enrichment.

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1. Introduction

Inducible defenses (ID) can be understood as reversible, phenotypic changes of prey traits which provide protection against predation, and are triggered by environmental cues often associated with higher predation risk (Harvell, 1990; Harvell and Tollrian, 1999). Different biological forms of ID

have been reported to occur over a wide range of taxa, such as changes in cell shape by protozoans (Kuhlmann and Heckmann, 1985), colony formation by green algae (Hessen and van Donk, 1993), spine formation by rotifers (Gilbert, 1966) and cladocerans (Krueger and Dodson, 1981), release of chemicals by angiosperms (Karban and Carey, 1984), behavioral modifications in zooplankton (Lampert, 1989) and tadpoles

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Table 1 – Description of parameters used in the model

	$i = x$	$i = y$	Unit	Short definition
M_i	1	–	dl	Metabolic cost
E_i	–	1	dl	Handling-time ID effectiveness
F_i	1	1	dl	Feeding cost/attack-rate ID effectiveness
ε_i	0.36	0.5	dl	Conversion efficiency
a_i	0.77	2.71	(mg C day) ⁻¹ dm ³	Basal attack rate
λ_i	0.1	0.1	(mg C day) ⁻¹ dm ³	Self-limitation coefficient
f_i	0.47	0.25	day ⁻¹	Feeding requirement for zero growth
h_i	0.5	0.83	day	Basal handling time
u	0.1		mg C dm ⁻³	Predators level for half defense level
v	10		dl	Abruptness of defense response
R	5		mg C dm ⁻³	Prey resource

dl: dimensionless. Most parameter values were taken from Vos et al. (2004a).

(Skelly and Werner, 1990), and body shape changes in tadpoles (Smith and Van Buskirk, 1995) and fish (Brönmark and Miner, 1992) among others (see also Tollrian and Harvell, 1999; Lass and Spaak, 2003).

Whereas the ecology of ID has been reasonably well studied at the organism level, there is scarcity of experimental evidence (Altwegg et al., 2004; Verschoor et al., 2004; Van der Stap et al., 2006) and theoretical studies (Frank, 1993; Abrams and Walters, 1996; Ramos-Jiliberto et al., 2002; Ramos-Jiliberto, 2003; Vos et al., 2004a,b; Kopp and Gabriel, 2006) addressing the effects of ID on population and community dynamics, despite the ubiquity of its occurrence. Nonetheless, those available works agree in that inducible defenses can damp population oscillations, and prevent destabilization of systems subjected to enrichment.

To our knowledge, no studies have focused on whether different biological mechanisms of ID could lead to different system dynamics. Any defense by definition interferes with the predation process at a given step within the sequence from searching to assimilation of the prey by the predator. For example, while predator avoidance mechanisms make difficult for predators to detect or capture a prey item, the development of body spines will interfere with the ingestion step after capturing. Therefore, we can conveniently classify defenses into two categories: pre-encounter and post-encounter (Sih, 1987) ones. On the other hand, an ID should bear some fitness costs when it is exhibited (Harvell and Tollrian, 1999), and the possible mechanisms responsible for a given cost can also fall into broad classes. Behavioral ID are usually associated with a feeding decrease of the prey, because the use of safe places or the display of a safe behavior often trades-off with food availability (Stich and Lampert, 1981). However, morphological or physiological mechanisms of ID can bear a metabolic cost derived from energy allocation to the development of defensive structures and processes (Barry, 1994).

Since much of contemporary predation theory rest on the hyperbolic functional response hypothesis attributed to Holling (1959), we shall make use of his two-parameter disk equation as the base from which we derive a more complex function, assuming that a pre-encounter ID will affect the predator attack rate while a post-encounter ID will alter the handling time of a prey unit (see next section). Therefore, in the present work we present and analyze a one-prey-one-predator model that includes two alternative types of ID:

one acting through decreasing attack rate of predators (pre-encounter ID), and the other one acting through increasing handling time on prey (post-encounter ID). The model also discriminates between metabolic and feeding costs associated with the ID, making possible a representation of behavioral predator avoidance versus morphological defenses, among other possible forms of ID. Our aim is to reveal the dynamic consequences of different kinds of ID on a minimal realistic system which exhibit periodic oscillation in the basal undefended case.

2. The model

We begin constructing the model on the base of a Lotka–Volterra–Bazykin template of the form (see Turchin, 2003; Ramos-Jiliberto, 2005):

$$\frac{dN_i}{dt} = N_i(g_i(\phi_i) - \lambda_i N_i) - \phi_{i+1} N_{i+1} \quad (1)$$

where N_i is the population size (in biomass) of a species with trophic level i , ϕ_i the per unit-predator ingestion rate (i.e. functional response or extraction function) of species i on its resource of level $i - 1$, the function g_i is the conversion function of ingested resources to population growth, and λ_i is the logistic self-limitation coefficient (see Table 1 for a summary of parameters utilized). The reason for including self-limitation is two-fold. First, it is more general since λ_i can be set to any value including zero. Second, self-limitation is known to be found in nature, among other things, due to intraspecific competition for fixed resources or to intraspecific inhibition of population growth caused by waste-products released by the individuals. For example, increasing population density of phytoplankton drives decreasing light availability for photosynthesis (Agustí, 1991; Kamenir, 1992), whereas in zooplankton inhibition has been reported as crowding effects in cladocerans (Burns, 2000; Mitchell and Carvalho, 2002; Lüring et al., 2003) and autotoxins production in rotifers (Kirk, 1998; Van der Stap et al., 2006). The interacting effects between self-limitation and ID was theoretically investigated in Ramos-Jiliberto (2003), and those results showed that self-limitation increases stability under all tested conditions. In the present work, we set the values of λ_i to be reasonably small and giving rise to an oscillatory dynamics bounded to biologically plausible ranges.

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