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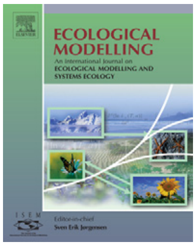

Pre-encounter versus post-encounter inducible defenses in predator–prey model systems

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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 multidimensional 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	$(\text{mg C day})^{-1}\,\text{dm}^3$	Basal attack rate
λ_i	0.1	0.1	$(\text{mg C day})^{-1}\,\text{dm}^3$	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):

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

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; Lürling 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.

The extraction function considered here is a Holling type-II also called disk equation:

$$\phi_i = \frac{1}{(A_i N_{i-1})^{-1} + H_i} \tag{2}$$

where A_i is the attack rate and H_i is the handling time of a prey item. This equation (functional response) is said to be a well-supported generalization in population ecology (Turchin, 2003) and can also be derived through adaptive considerations (Tschirhart, 2004). For simplicity, the conversion function is considered to be linear:

$$g_i(\phi_i) = \varepsilon_i(\phi_i - \phi_i^0) \tag{3}$$

where ε_i is the conversion efficiency of food consumed to growth and ϕ_i^0 is the per capita consumption requirement for zero growth (i.e., a population maintenance requirement). This form of presenting the conversion function allows for incorporating different amounts of energetic supply and demand in an explicit way.

2.1. *Incorporating ID*

We use here a sigmoid function D_i which represents the level of defenses exhibited by a prey population of trophic level i:

$$D_i = \frac{N_{i+1}^{v}}{N_{i+1}^{v} + u^{v}} \tag{4}$$

Defense level $D_i \in [0, 1]$ is dependent on the population size of predators (N_{i+1}). Shape parameters are u and v, which determine, respectively, the predator density for half-level defenses, and the abruptness of the defensive function. This function is inverse to the one used in previous works (Ramos-Jiliberto and González-Olivares, 2000; Ramos-Jiliberto et al., 2002; Ramos-Jiliberto, 2003), and of the same form to the one used by Vos et al. (2004a,b) for modeling induction rate of prey defenses. It should be noted that (4) is one among many possible forms of representing defense (or invulnerability) level at a population scale. For example, in Vos et al. (2004a,b) prey individuals can exhibit either a defended or an undefended phenotype, and thus the population is structured into two discrete states and it is represented by two state-variables. In this work we consider an average defense level given by (4), that can represents either an entire range of individual defense level, or the proportion of defended units if individuals present only two discrete states of defenses. In this way we avoid increasing the dimension of the system, and keep the model structurally closer to classical bidimensional predator–prey systems.

Here we discriminate between those defenses that act through decreasing the attack rate (e.g. behavioral avoidance) and those acting through increasing difficulty to handling (e.g. morphological structures which decrease ingestion probability after encounter). For those defenses acting via decreasing attack rate, we set:

$$A_i = a_i[1 + (F_i - 1)D_{i-1}] \tag{5}$$

where attack rate of consumer of trophic level i on prey of level $i-1$ decreases linearly with defense level D_{i-1} exhibited by the prey. Upper and lower limits of A_i (moving D_{i-1}) are given, respectively, by the parameter a_i and the product a_iF_i. When $F = 0$, A_i decreases with D_{i-1}, when $F = 1$ then there is no effect of D_{i-1} on A_i. Therefore $F_i \in [0, 1]$ represents the relative decreasing of A after the induction of full defenses.

Conversely, defenses acting via increasing handling time will affect H_i by

$$H_i = h_i[1 + (E_i - 1)D_{i-1}] \tag{6}$$

where h_i is the basal (unaffected) value of H_i and h_iE_i is the maximal value of H_i when $D_i = 1$. Therefore, E_i (being larger or equal than 1) represents the relative increment of H_i as a consequence of the defense. For a one-prey–one-predator system, increasing handling time is a good and simple representation of the primary action of post-encounter defenses. Nevertheless, if more than one type of prey is included in the model, the correct form of representing post-encounter defenses is via increasing handling time and reducing attack-rate simultaneously. We verified that (6) yields the same qualitative output than using more complex functions which include attack-rate decrease, and therefore for our purposes we equate post-encounter ID with handling-time based ID in order to avoid any unnecessary complication.

Taking Eqs. (5) and (6) into (2) for the feeding of a unit predator (population size y) on the prey (population size x), and dropping the subscript of D_i renders:

$$\phi_y = \frac{1}{(a_y[1 + (F_y - 1)D]x)^{-1} + h_y[1 + (E_y - 1)D]} \tag{7}$$

where D is given by (4). This functional response incorporates both possible forms of ID.

2.2. *Costs of ID*

As long as the prey develops defenses after induction by predator density, different kind of costs can take place . We discriminate into two costs, the first being a metabolic cost consisting in an increase of the maintenance requirement ϕ_i^0:

$$\phi_x^0 = f_x[1 + (M_x - 1)D] \tag{8}$$

where f_x is the basal (unaffected) value of ϕ_x^0 (when $D = 0$) and $M_x \geq 1$ is the relative increment of the maintenance requirement with D. The second kind of cost considered here is a feeding cost, assumed to decrease the encounter rate between the defended prey and its own resource:

$$A_x = a_x[1 + (F_x - 1)D] \tag{9}$$

where a_x is the unaffected value of A_x (when $D = 0$) and $F_x \in [0, 1]$ is the relative decrease of the prey-resource encounter rate. When $F_x = 0$, then $a_x(1 - D)$ defines the decrease of the prey-resource encounter rate.

Through including (9) into (2), and the latter together with (8) into (3), we obtain:

$$g_x = \varepsilon_x([(a_x[1 + (F_x - 1)D]R)^{-1} + h_x]^{-1} - f_x[1 + (M_x - 1)D]) \tag{10}$$

where R is basal resource density. By using (7) and (10), and replacing in (3) and (1), we get the system under study:

$$\begin{aligned}\frac{dx}{dt} &= x\varepsilon_x([(a_x[1 + (F_x - 1)D]R)^{-1} + h_x]^{-1} - f_x[1 + (M_x - 1)D]) \\ &\quad - \lambda_x x^2 - y[(a_y[1 + (F_y - 1)D]x)^{-1} + h_y[1 + (E_y - 1)D]]^{-1}\end{aligned}$$

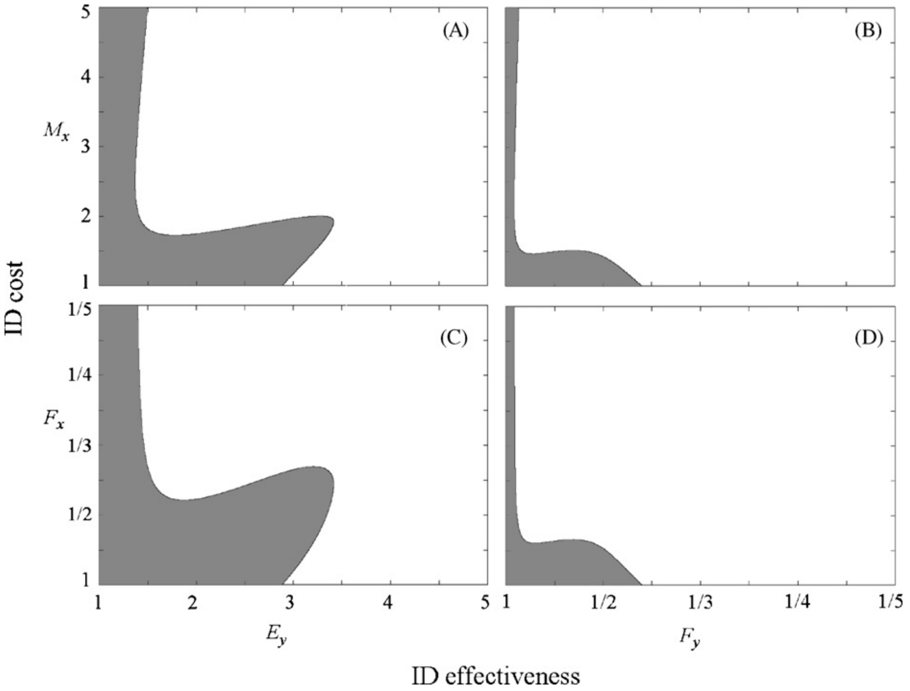

Fig. 1 – Stability domains for ID effectiveness vs. costs. (A) Handling-time based ID with metabolic cost, (B) attack-rate based ID with metabolic cost, (C) handling-time based ID with feeding cost, and (D) attack-rate based ID with feeding cost. Shaded area indicates instability of the equilibrium points and occurrence of periodic oscillations. The axis scale is presented in a way that the magnitude of cost and effectiveness of ID increases from the origin towards the upper-right corner.

$$\frac{dy}{dt} = y\varepsilon_y([(a_y[1+(F_y-1)D]x)^{-1} + h_y(1+(E_y-1)D)]^{-1} - f_y) - \lambda_y y^2 \tag{11}$$

with

$$D = D(y) = \frac{y^v}{y^v + u^v} \tag{12}$$

note that in absence of ID, our model reduces to the Bazykin model:

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - \frac{A_y xy}{1 + A_y H_y x},$$

$$\frac{dy}{dt} = \varepsilon_y \frac{A_y xy}{1 + A_y H_y x} - \mu y - \lambda_y y^2 \tag{13}$$

with constants $r = \varepsilon_x((A_x R/1 + A_x H_x R) - \phi_x^0)$, $K = r/\lambda$, and $\mu = \varepsilon_y \phi_y^0$. Note that (11) possess structural homogeneity since all populations obey the same general rules (Getz, 1994; Berryman et al., 1995), and at the same time it allows for a direct manipulation of the parameter values representing costs and basal resource level.

2.3. Analysis

We perform numerical analyses with the help of the software XPP-Auto Version 5.3 (Ermentrout, 2002) using the Stiff integration algorithm for phase-plane analysis. The embedded package Auto (Doedel, 1984) performs one-parameter and two-parameter continuation routines for bifurcation analyses. For one-parameter bifurcation diagrams, only densities of prey (x) are shown since the qualitative behavior of both variables is coupled. Starting parameter values (Table 1) were obtained from published experimental reports of a freshwater planktonic system (Vos et al., 2004a) and converted to the units utilized here. We also performed sensitivity analyses for the non-target parameters (varying 50% up and down the starting value) in order to check for the robustness of the results.

3. Results and discussion

3.1. Effectiveness and costs of ID

The basal state of our system (no ID displayed) is given after setting all ID effectiveness and costs equal to one. At this point, there exists one interior equilibrium point, which is unstable and it is surrounded by a stable limit cycle. An analytical study of such a system is given in Hainzl (1988). Our procedure was to perturb this basal system through incorporating ID effectiveness, costs, and decreasing resource availability. The results showed noticeable changes concerning the stability of this point and the periodic orbits around it.

In Fig. 1 continuation sets of Hopf bifurcations are shown on the parameter space formed by the four types of cost-defense combinations. Fig. 1A shows effectiveness of a handling-time-based ID (E_y) versus metabolic cost M_x (this parameter combination representing morphological ID). Fig. 1D shows the Hopf bifurcation continuation on a F_y versus F_x plane, representing avoidance ID (decreased predator attack-rate involving a feeding cost). For completeness, the stability domains of the other two combinations are also illustrated (Fig. 1B and C), although they do not give much additional information (see below).

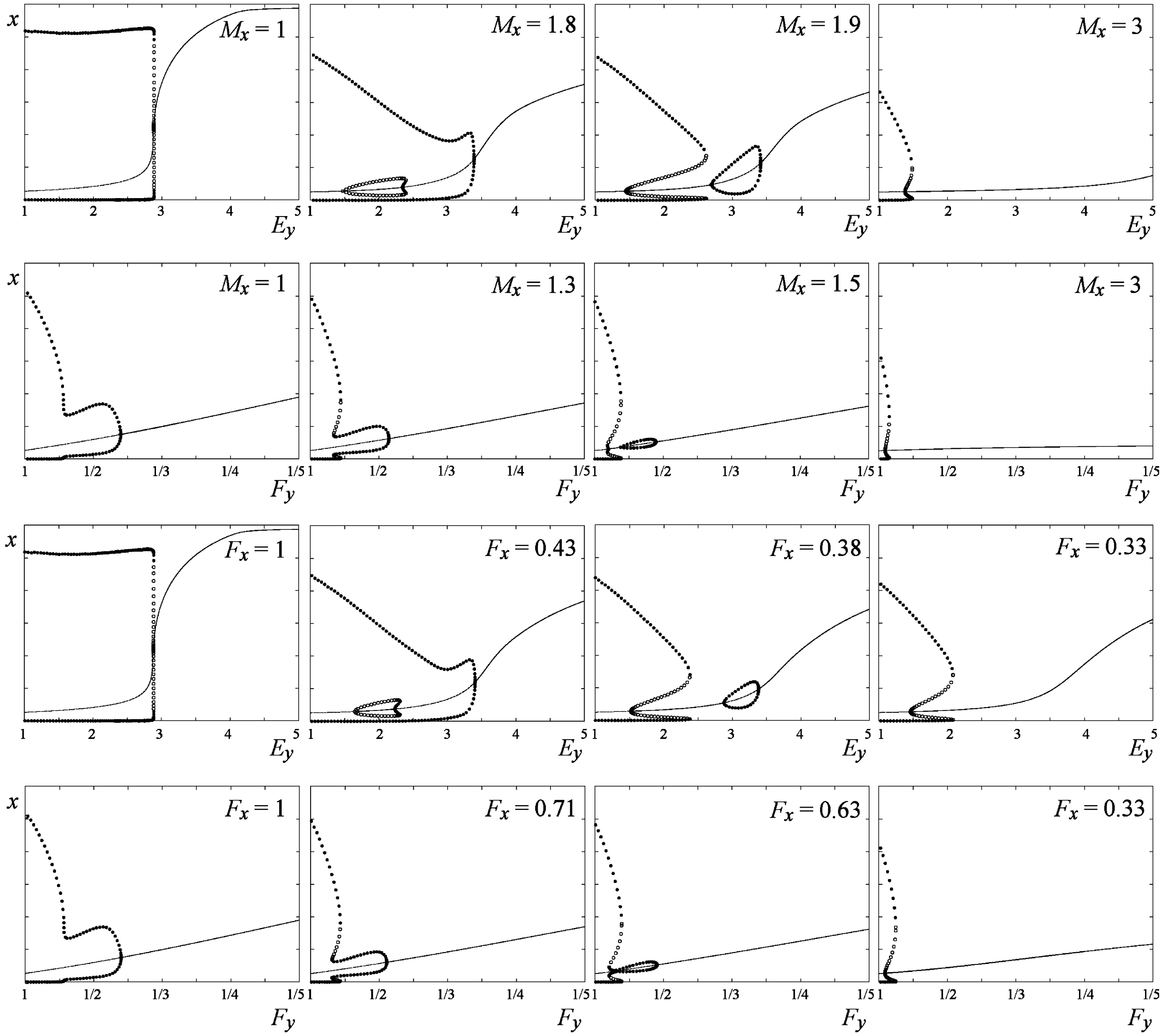

Fig. 2 – Bifurcation diagrams corresponding to horizontal sections of plots in Fig. 1. Hereafter, continuous lines indicate equilibrium points, closed circles represent stable periodic orbits, and open circles represent unstable periodic orbits.

Since the above-mentioned plots are unable to reveal dynamics in more detail, we dissect them into one-parameter continuation diagrams (Fig. 2) which uncover regions with more rich and interesting dynamics. These graphs show the equilibrium density points of the prey (continuous lines) and the maximal and minimal values of stable (filled circles) or unstable (open circles) periodic oscillations. Unstable equilibrium points are surrounded by stable orbits and thus nearby trajectories will approach the periodic attractor. Nevertheless, for a given set of parameter values, two stable periodic attractors can coexist separated by an unstable orbit which acts as a repellor (see the second column). Also, one stable periodic attractor can coexist with a stable point (third graph of first row, see below for further comments).

Roughly speaking, both defense effectiveness (E_y and F_y) and costs (F_x and M_x) tend to stabilize the populations. More precisely, through increasing the values of defense effectiveness and cost the amplitude of oscillations decreases and the equilibrium point which is initially unstable is made stable. When the cost of ID is low, a considerable level of ID effectiveness is needed to stabilize the system. Conversely, at higher levels of cost (i.e. $M_x > 2 < F_x$) a slight increase in ID effectiveness is enough to stabilize the point.

At intermediate level of cost, increasing ID effectiveness can act either stabilizing or destabilizing the system (see Fig. 1A) and a complex set of dynamic output is obtained through varying E_y. A single stable point occurs for high levels of ID effectiveness and for moderate to high levels of cost in combination with moderate levels of ID effectiveness. A single limit cycle exists with very low or null ID effectiveness and for moderate ID effectiveness combined with low cost. Between these two single-attractor zones, a transitional region is found where two attractors coexist, being them either two stable orbits separated by an unstable one, or a stable point and a stable orbit also separated by an unstable orbit. In ecological terms, this means that there exist sets of parameter values and initial conditions for which slight perturbations exert a strong effect on the long term behavior of the population trajectories.

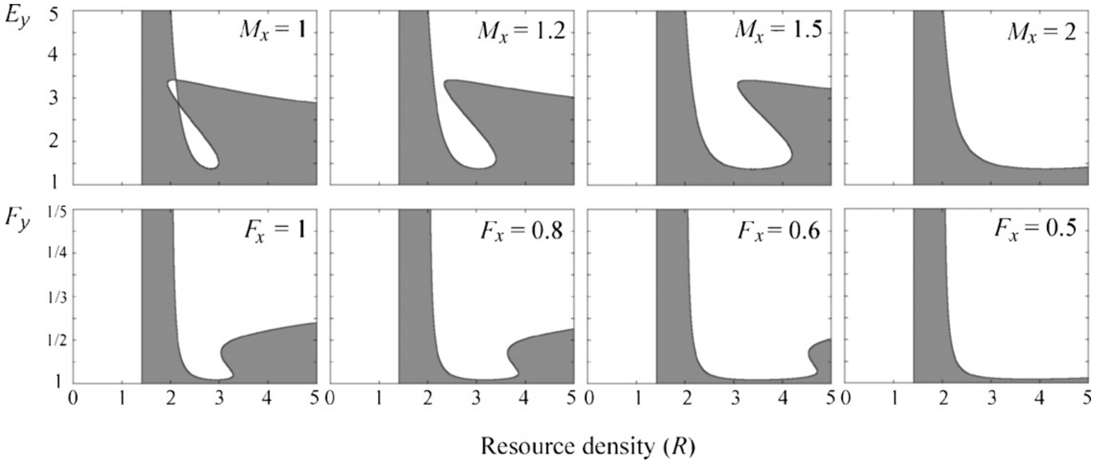

Fig. 3 – Stability domains for resource level vs. ID effectiveness. The sequence of plots show the effects of increasing ID costs. Upper row: handling-time based IDs with metabolic cost; lower row: attack-rate based ID with feeding cost.

Therefore, complex shifts between oscillatory and monotonic behavior is expected if some level of stochasticity is added to the system. This zone of complex dynamics appears larger for handling-time based ID relative to the attack-rate based ID, irrespective of the kind of cost involved. Moreover, alternations between stabilization and destabilization occur through varying ID effectiveness or cost for the case of handling-time based ID. In contrast, for attack-rate based ID this only occurs when varying ID effectiveness. Therefore, the kind of cost involved appears to have little effect on the qualitative dynamics, but the kind of defense plays a significant role for the asymptotic behavior of the populations, specially in some regions of the parameter space.

3.2. *Enrichment*

Recently it has been suggested that IDs prevent the paradox of enrichment, i.e. prevent destabilization caused by increasing the availability of basal resources of the community (Vos et al., 2004b). Here we test this statement in our model through varying the resource density together with ID effectiveness, and then incorporating different levels of costs. Originally, the concept of enrichment refers to an increase in limiting nutrients or energy (Rosenzweig, 1971), and we equate this to increase the value of parameter R. Note, nevertheless, that this is not mathematically equivalent to decrease the carrying capacity parameter (K in (13)) as usually done (Rosenzweig, 1971; Vos et al., 2004b).

In Fig. 3 we show the resulting stability domains in the parameter space conformed by resource level and ID effectiveness at increasing values of metabolic (M_x) and feeding (F_x) costs. On the abscissa it rests the basal condition of no ID, which is shown in more detail in Fig. 4 by means of a one-parameter bifurcation diagram. In this and the next figure, there appears an upper continuous curve showing saddle (unstable) points outside the positive quadrant. Therefore, those curves do not have implications for the dynamics under a biologically plausible scenario, and the population trajectories will approach either a point attractor or a periodic attractor depending on the amount of basal resources R. When no ID occur, increasing food levels drives to destabilization of the equilibrium point giving rise to periodic cycles with increasing amplitude, as predicted by the paradox of enrichment. At very low resource level, nevertheless, the predator population or both predators and prey fall to extinction. When adding ID, increasing resources makes the dynamics more complex (Fig. 5), with two attractors coexisting for some resource levels. Note that at higher ID effectiveness a bistability phenomenon is revealed by the coexistence of two point attractors separated by a saddle point, which can be observed as a s-shaped continuous curve. Also, hysteresis is observed under various parameter values. Further enrichment (i.e. increasing R up to > 10) did not lead to new bifurcations.

As ID effectiveness is higher and costs are more severe, high resource levels maintain the system stable. The more complex scenario occurs when ID effectiveness is moderate while costs are null or low (Figs. 5 and 6), since high resource levels drive to destabilization but moderate levels produce two simultaneous attractors and hysteresis. It was found the coexistence

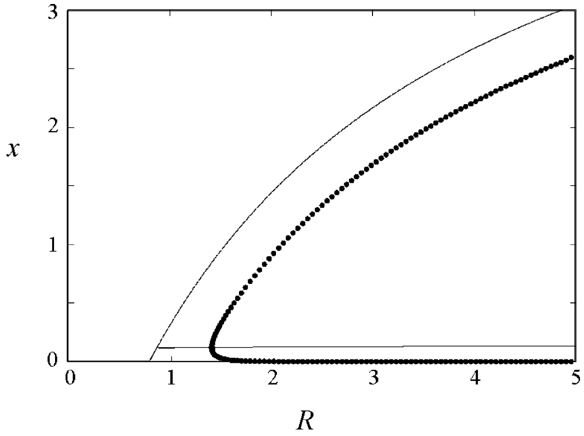

Fig. 4 – Bifurcation diagram corresponding to horizontal sections of plots in Fig. 3 at $E_y = F_y = 1$, i.e. effects of resources on the system with no ID. In this and subsequent figures it is shown an upper thin-line hyperbola which indicates equilibria at $y = 0$.

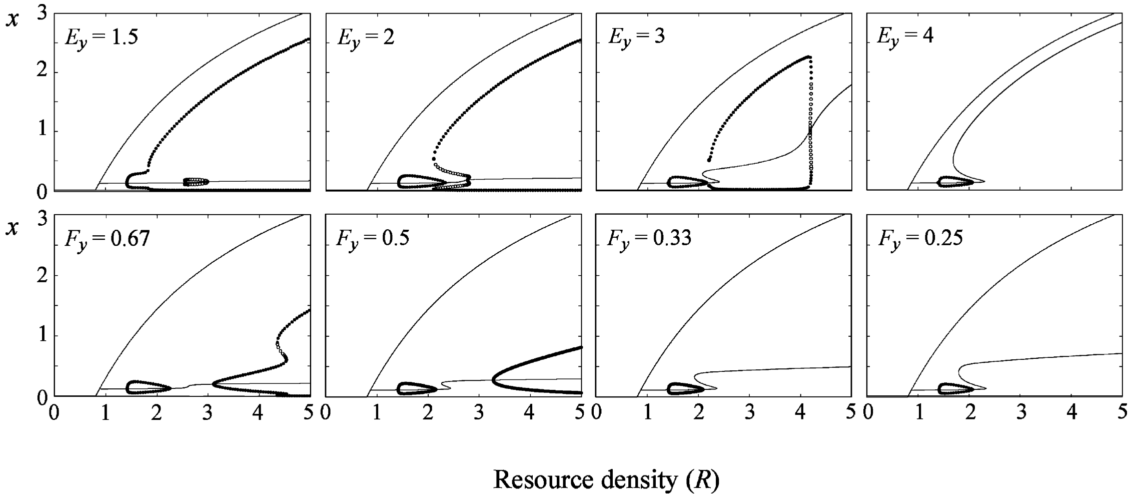

Fig. 5 – Bifurcation diagrams corresponding to horizontal sections of plots of Fig. 3 at $M_x = F_x = 1$, i.e. with no costs. Upper row: handling-time based IDs; lower row: attack-rate based ID.

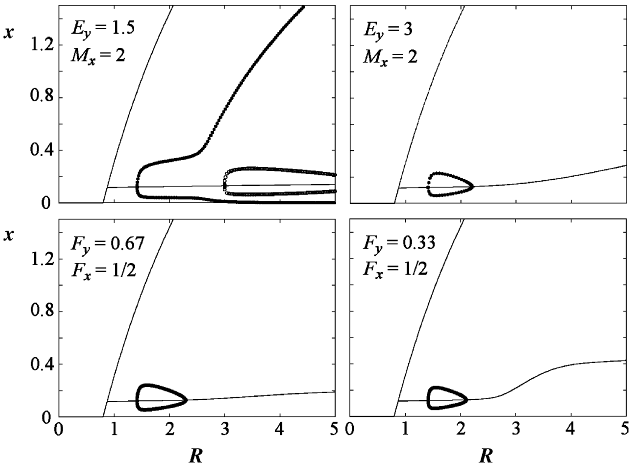

Fig. 6 – Same as Fig. 5, but considering two selected ID effectiveness and one level of costs.

of two stable periodic orbits or one stable periodic orbit and one stable point, where the two domains of attraction were separated by an unstable periodic orbit (Figs. 5 and 6). Reversing the type of cost does not change noticeably the stability domains obtained for each type of ID.

Our results show that at moderate and high ID effectiveness, a further stabilization occur after adding costs. Nevertheless, at low ID effectiveness, the effect of cost is dependent on the type of strategy. In Fig. 6 we show that handling-time based ID with metabolic cost ($M_x = 2$) in the region of low effectiveness ($E_y = 1.5$) exhibits a stable orbit, a stable equilibrium point, and an unstable periodic orbit between them when resources are high. By contrast, attack-rate based ID with feeding cost show the most of the parameter space with a stable equilibrium. This result reveals that the interaction effect between cost of ID and resource level differs for handling-time and attack-rate based IDs.

Although most of the parameter values were selected from empirical results, further sensitivity tests were made for every other parameter not analyzed in this section in order to ensure some generality of our results. For most parameter changes, the qualitative predictions remain the same. Nevertheless, parameters λ_i, u and v showed to have significant

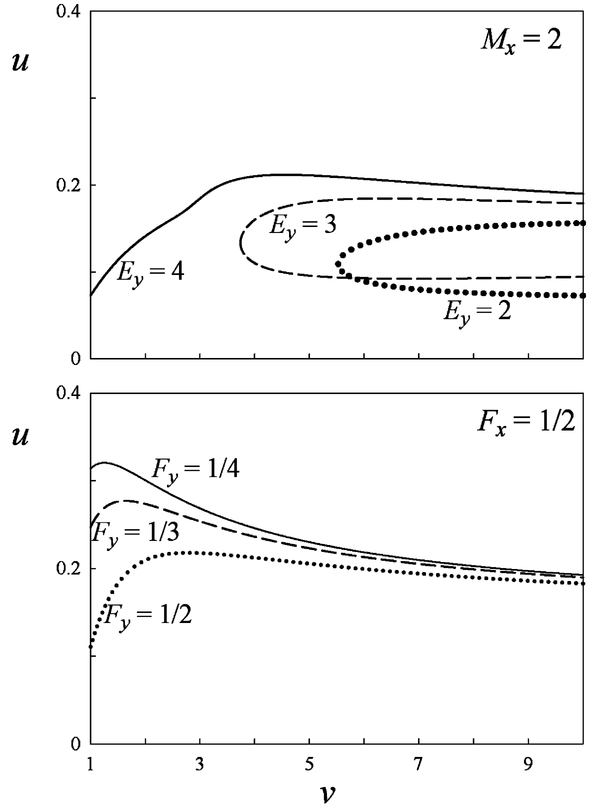

Fig. 7 – Each of the lines, resulting from different values of ID effectiveness and a fixed amount of cost, divides the parameter space u vs. v into two domains of attraction. Unstable equilibria above the lines, stable equilibria below the lines. Upper plot: handling-time based ID with metabolic cost; lower plot: attack-rate based ID with feeding cost.

effects on the dynamics. Since our focus is on the defense effectiveness, costs and resource levels, and the role of self-limitation was already exposed (Ramos-Jiliberto, 2003) we will briefly examine the effects of u and v which define the shape of the defense function.

The role of the shape parameters u and v is shown in Fig. 7 for handling-time and attack-rate IDs. Note that high u values maintain the system oscillatory, independent on the ID effectiveness. The value of parameter v is important specially for handling-time based IDs, since higher values determines a more complex set of stability basins.

3.3. *Concluding remarks*

It is becoming clear that delayed negative feedback is a general mechanism promoting endogenous periodic oscillations in real populations (Berryman, 2002). Delayed negative feedback can be due to multiples causes, but the best recognized is predator–prey (including host-parasite) interaction. Since any natural population is either prey (host) or predator (parasite), we can find the seed for population cycles in any natural community. Nevertheless, available time series information reveals that only 30% of animal populations exhibit cycles (Kendall et al., 1998). Thus, in order to understand and explain the dynamics of natural communities it should be useful to know what kind of endogenous population processes prevent an unstable behavior. In particular we are interested to address what kind of feedback structure can be generated by considering more realistic properties of trophic interactions, such as the influence of plastic defensive traits, and under which conditions model populations are expected either to cycle or to remain unchanged through time.

Ecological consequences of antipredator defenses have been studied in a population context since several decades, formerly in the form of refuge use by a fixed number or fraction of the prey population (Maynard-Smith, 1974; Murdoch and Oaten, 1975; Harrison, 1979; Ives and Dobson, 1987; González-Olivares and Ramos-Jiliberto, 2003; Srinivasu and Gayatri, 2005) or habitat segregation (e.g. Maionchi et al., 2006). Compared with equivalent models in which no defenses are included, those works often showed that defenses have a stabilizing effect on the predator–prey dynamics, although other results show no such simple pattern (McNair, 1986; Collings, 1995). More recently, it has been empirically demonstrated that many antipredator responses are phenotypically plastic traits which operate through modifying behavior, morphology or physiology in response to predation risk signaling (see Tollrian and Harvell, 1999) and therefore a time-varying number of prey is defended in response to cues released by predators. An ecological system containing prey exhibiting inducible defenses present a more complex feedback structure in comparison to systems which do not exhibit such responses, specially if costs are involved. Therefore, it is plausible to hypothesize that the dynamics of populations should be sensitive to the occurrence of IDs.

The recent literature dealing with ID in population models considers development of defenses as a decrease in vulnerability to predation, but the representation of how the ID modifies the consumption process and how the costs affect the growth rate is diverse. In Vos et al. (2004a,b) it was considered a prey population as structured into two states that differ in vulnerability to predators, and the transition rates between both states were regulated by predator density. There, the model primarily assumes that defense acts through decreasing availability of more edible prey, and the cost was assumed to increase a death rate parameter. In the mentioned model ID was considered to be handling-time based. Conversely, Ramos-Jiliberto et al. (2002) and Ramos-Jiliberto (2003), considered the single-variable prey population possessing an average vulnerability which was dependent on predator density. In these works we considered the ID to affect prey availability for predators and therefore those models are equivalent to the attack-rate based ones, with both metabolic and feeding costs. Whereas the works Vos et al. (2004a,b) focused on the effects of ID on the stability changes and biomass responses after enrichment, Ramos-Jiliberto (2003) focused on the interaction between ID and density-dependence under two types of costs. Both lines of research developed models with some different assumptions, and the most important are: the inclusion or not of self-limitation in the upper trophic level, and the number of state variables representing a single prey species.

Despite the different systems (equations) of study, the present work is in line with Vos et al. (2004a,b) and Ramos-Jiliberto (2003) in that: (a) ID promote stability of food chains, (b) the associated costs also promote stability under most conditions, and (c) ID resolve the paradox of enrichment, in agreement with the earlier work (Abrams and Walters, 1996), as well as with Verschoor et al. (2004) and Van der Stap et al. (2006) which provided empirical evidence that ID decreases the amplitude of oscillations in bitrophic and tritrophic systems.

In this work, our main focus was to analyze population dynamics under two clearly distinguished hypothesized mechanism of ID: handling-time based and attack-rate based ID subjected either to metabolic or feeding cost. Both types of cost exhibit a similar effect on the dynamics of our bidimensional model, but we expect that different costs will produce different dynamics in a more complex model community, where resources are considered as an additional state-variable. Under that scenario, metabolic costs will directly reduce growth rate of prey, while feeding cost involves both a reduction in prey growth rate and an increase in resource growth (Peacor, 2002). Our results reveal that the distinction between handling-time based IDs (e.g. morphological defenses) and attack-rate based IDs (e.g. behavioral defenses) is not unimportant, since they define domains of attraction with different size and shape within the studied sections of the multidimensional parameter space. Roughly speaking, handling-time based 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.

Our results confirm that predator–prey systems behave quite different if one considers explicitly the occurrence of ID, and that the systems are sensitive to the type of defense exhibited by the prey, in combination with the availability of basal resources. It would be desirable if experiments were performed in order to test whether this ubiquitous property of prey (ID) really impose such a large effect on real populations.

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