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

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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.

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 Sirot, 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

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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:

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

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

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

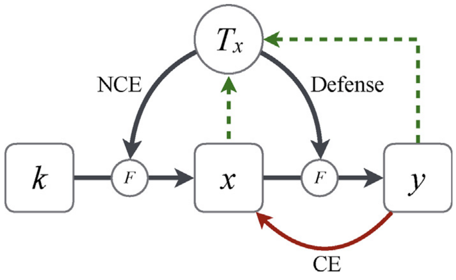

Fig. 1. Conceptual model of prey defenses. Predators of abundance y consume prey of abundance x which in turn consume resources of abundance k. Consumption rate is governed by functional responses F. Prey x exhibit some set of traits T_x which suppresses predator's functional response F and consumptive 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).

$$X_\mu : \begin{cases} \dfrac{dx}{dt} &= r\Big(1-\dfrac{x}{K}\Big)x - q\,x(1-\delta y)y \\ \dfrac{dy}{dt} &= (p\,x(1-\delta y)-c)y \end{cases} \tag{3}$$

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

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

The equilibrium points are $P_0 = (0, 0)$, $P_K = (K, 0)$ and $P_e = (x_e, y_e)$, with $y_e = \frac{rp}{cq}\left(1-\frac{x_e}{K}\right)x_e$, 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

Table 1
A classification of triggering mechanisms of antipredator defenses.

Assumption	Simple expression	Biological meaning	Key references
$\frac{\partial R}{\partial x}=0$, $\frac{\partial R}{\partial y}=0$	$R=\delta$	Constitutive defenses	
$\frac{\partial R}{\partial x}=0$, $\frac{\partial R}{\partial y}>0$	$R=\delta y$	Induced defenses	This study
$\frac{\partial R}{\partial x}>0$, $\frac{\partial R}{\partial y}=0$	$R=\delta x$	Group defenses	Not found
$\frac{\partial R}{\partial x}>0$, $\frac{\partial R}{\partial y}>0$	$R=\delta xy$	Encounter-driven defenses	Not found
$\frac{\partial R}{\partial x}<0$, $\frac{\partial R}{\partial y}=0$	$R=\delta/x$	Fixed-capacity refuges	
$\frac{\partial R}{\partial x}<0$, $\frac{\partial R}{\partial y}>0$	$R=\delta y/x$	Risk-induced defenses	lez-Olivares and Ramos-Jiliberto (2004), Haque et al. (2014); lez-Olivares and Ramos-Jiliberto (2004), Haque et al. (2014)

asymptotically stable, if and only if, $c\geq pK$. In the rest of this article we show our main analytical results for $\delta>0$.

3. Main results

To simplify the calculus we first perform a reparameterization and time rescaling of system (3), establishing the properties presented below. Relevant demonstrations of the stated model properties are given in Appendix A. To help the reader non-familiar with mathematical jargon, in the Discussion section we mention the parts of our results (Lemmas and Theorems presented in this section) that serve as the basis for the main conclusions of our study.

Proposition 1. *System (3) is topologically equivalent to*

$$Z_\eta:\begin{cases}\dfrac{du}{d\tau} &= (1-u-(1-Nv)v)u\\ \dfrac{dv}{d\tau} &= B(u(1-Nv)-C)v\end{cases} \tag{5}$$

with $\eta=(B,C,N)\in\mathbb{R}^2_+$, $B=\frac{pK}{r}$, $C=\frac{c}{pK}$ *and* $N=\delta\frac{r}{q}$.

Remark 2. 1. We have constructed the diffeomorphism (Chicone, 2006) $\varphi:\overline{\Omega}\times\mathbb{R}\longrightarrow\Omega\times\mathbb{R}$, so that $\varphi(u,v,\tau)=\left(Ku,\frac{r}{q}v,r\tau\right)=(x,y,t)$.The Jacobian matrix of φ is $D\varphi(u,v,\tau)=\begin{pmatrix}K&0&0\\0&\frac{r}{q}&0\\0&0&r\end{pmatrix}$ As $\det D\varphi(u,v,\tau)=\frac{K\,r^2}{q}>0$, then φ is a diffeomorphism preserving the time orientation. The new vector field $Z_\eta=\varphi\circ X_\mu$ associated to differential equations system (5), is defined at

$$\overline{\Omega}=\left\{(u,v)\in\mathbb{R}^2_0/u\geq 0,v\geq 0\right\}=\mathbb{R}^+_0\times\mathbb{R}^+_0. \tag{6}$$

The equilibrium points of system (5) are

$$O=(0,0),Q_1=(1,0)\ \text{ and } Q_e=\left(u_e,\frac{1}{C}(1-u_e)u_e\right), \tag{7}$$

where $u_e$is a solution of the cubic polynomial equation

$$p(u)=Nu^3-Nu^2+Cu-C^2=0 \tag{8}$$

The equilibrium point Q_e lies in $\overline{\Omega}$, if and only if, $u_e<1$.

Using the Descartes Rule, it is easy to see that Eq. (8) may have up to three positive roots, but it always has a positive real root denoted by $u_1=E$. For the point Q_e to be positive, it must be satisfied that $E<1$.

From the quotient between $p(u)$ and the binomial $u-E$ it could be possible to obtain the other two solutions, as the reader could verify (Proof of Lemma 5, Appendix A).

To determine the nature of the hyperbolic equilibrium point we need the Jacobian matrix of system (5) which is

$$DZ_\eta(u,v)=\begin{pmatrix}1-2u-v+Nv^2 & -(1-2Nv)u\\ B(1-Nv)v & B(u-C-2Nuv)\end{pmatrix} \tag{9}$$

Further properties of system (5) are:

Lemma 3. *(a) The set* $\overline{\Gamma}=\left\{(u,v)\in\overline{\Omega}/0\leq u\leq 1,\ 0\leq v\leq\frac{1}{N}\right\}$ *is an invariant and compact region.(b) Solutions are bounded.*

After showing that the trajectories are bounded, we can consider that system (5) is a well-posed model (Berryman et al., 1995), since the point $(0,\infty)$ in the compactified system (Perko, 2001) is a saddle point.

We note that if $1-Nv<0$, then $\frac{du}{d\tau}>0$ and $\frac{dv}{d\tau}<0$. In such a case system (5) would lose its biological sense in the frame of a predator–prey interaction.

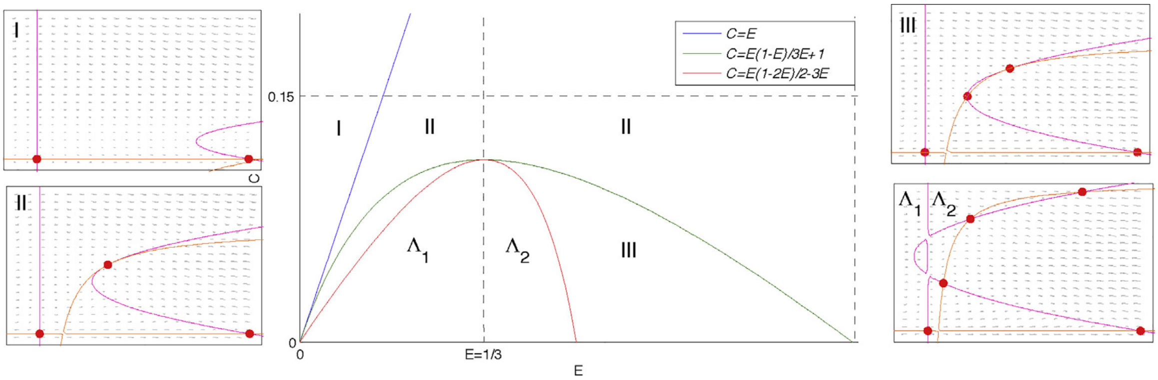

Fig. 2. The bifurcation curves defining the stability domains of the study model. In region I there is no interior equilibrium points, while one and two positive equilibria are found in regions II and III respectively. In regions Λ_1 and Λ_2 three equilibrium points exist.

Furthermore, for system (5), the set $\overline{\Gamma}$ is a compact region. Then the set

$$\Gamma = \left\{(u, y) \in \Omega / 0 \le x \le K, 0 \le y \le \frac{1}{\delta}\right\}$$

is a compact region for system (3). So, in both cases the Poincaré–Bendixon Theorem holds.

Lemma 4. *Nature of the equilibrium points located on the axesFor all parameter values we obtain that(a) The singularity* $(0, 0)$ *is a saddle point.(b) The singularity* $(1, 0)$ *is a saddle point.*

Lemma 5. *Number of positive equilibrium pointsFrom Eq. (8) we obtained:(a) It has a unique positive real root, denoted by* $u_1 = E < 1$, *if and only if* $D = -3EC - C - E^2 + E < 0$, *that is,* $E\frac{1-E}{3E+1} < C < E$,*(b) It has two positive real roots, one of them of multiplicity two, if and only if* $D = -3EC - C - E^2 + E = 0$, *or else,* $C = E\frac{1-E}{3E+1} < E$*; in this case,* $u_2 = u_3 = \frac{1-E}{2}$,*(c) It has three positive real roots, if and only if* $D = -3EC - C - E^2 + E > 0$, *or else,* $C < E\frac{1-E}{3E+1} < E$.

We note that the difference $C - E = \frac{E(1-E)}{3E+1} - E = -4\frac{E^2}{3E+1} < 0$. Thus, the curve $C = \frac{E(1-E)}{3E+1}$ locates under the straight line $C = E$.

Here we define in the parameter space the subset

$$\Lambda = \left\{(E, C) \in \left(\mathbb{R}_0^+\right)^2 / C < \frac{E(1-E)}{3E+1}\right\}$$

(a) If $(E, C) \in \Lambda$, then there are three positive values for the abscissa.
(b) If (E, C) is over the curve, this is, if $D = -3EC - C - E^2 + E = 0$ or $C = \frac{E(1-E)}{1+3E}$. Thus, there are two positive values for the abscissa, one of them of multiplicity two.
(c) If $(E, C) \in \left\{(E, C) \in \left(\mathbb{R}_0^+\right)^2 / \frac{E(1-E)}{1+3E} < C < E\right\}$, that is, (E, C) is between the curve and the straight line; therefore, a unique value for the abscissa exists.

For this abscissa value, the bifurcation diagram is given in Fig. 2.

From the quotient between the cubic polynomial $p(u)$ and the binomial $(u - E)$ we obtain a quadratic expression, and since the remainder is zero, we get $N = \frac{C(E-C)}{E^2(1-E)}$ (see Proof of Lemma 5, Appendix A). Then system (5), as a function of the new parameter E, can be written as

$$Z_\lambda : \begin{cases} \dfrac{du}{d\tau} &= \left(1 - u - \left(1 - \dfrac{C(E-C)}{E^2(1-E)}v\right)v\right)u \\ \dfrac{dv}{d\tau} &= B\left(u\left(1 - \dfrac{C(E-C)}{E^2(1-E)}v\right) - C\right)v \end{cases} \tag{10}$$

with $\lambda = (E, C, B) \in \left(\mathbb{R}_0^+\right)^3$ and $E < 1$, and equilibrium points $(0, 0)$, $(1, 0)$ and (u_e, v_e) that satisfies the nullcline equations $1 - u - \left(1 - \frac{C(E-C)}{E^2(1-E)}v\right)v = 0$ and $v = \frac{u-C}{uN} = \frac{(1-E)(u-C)E^2}{uC(E-C)}$.

The Jacobian matrix of system (10) is

$$DZ_\lambda(u, v) = \begin{pmatrix} 1 - 2u - v + \dfrac{C(E-C)}{E^2(1-E)}v^2 & \left(\dfrac{2C(E-C)}{E^2(1-E)}v - 1\right)u \\ B\left(1 - \dfrac{C(E-C)}{E^2(1-E)}v\right)v & B\left(u - C - \dfrac{2C(E-C)}{E^2(1-E)}uv\right) \end{pmatrix}.$$

Rescaling the time by $T = \frac{\tau}{E^2(1-E)}$, system (10) can be rewritten as

$$\tilde{Z}_\lambda : \begin{cases} \dfrac{du}{dT} &= \Big((1 - u)E^2(1 - E) - (E^2(1 - E) - C(E - C)v)v\Big)u \\ \dfrac{dv}{dT} &= B\Big(u(E^2(1 - E) - C(E - C)v) - C\Big)v, \end{cases} \tag{11}$$

for which we show some numerical examples in Appendix B.

Theorem 6. *Nature of the unique positive equilibriumAssuming* $D = -3EC - C - E^2 + E < 0$, *that is,* $E\frac{1-E}{3E+1} < C < E$, *then the unique positive equilibrium is globally asymptotically stable (Fig. A.1).*

Theorem 7. *Two positive equilibrium pointsFor* $D = -3EC - C - E^2 + E = 0$, *i.e.,* $C = \frac{(1-E)E}{3E+1}$, *there exist two positive equilibrium points (Fig. A.2). Then:*

(a) *The point* $(E, 3E + 1)$ *is an attractor*
(b) *The point* $\left(\frac{1-E}{2}, \frac{(E+1)(3E+1)}{4E}\right)$ *is a non hyperbolic saddle-node (Arrowsmith and Place, 1992).*
(c) *In particular if* $E = \frac{1}{3}$, *the three equilibrium points collapse and* $\left(\frac{1}{3}, 2\right)$ *is a non hyperbolic attracting point (Fig. A.3).*

In the following, we assume that $D = -3EC - C - E^2 + E > 0$, or $C < \frac{(1-E)E}{3E+1}$, thus, three positive equilibrium points exist in the phase plane.

Theorem 8. *Relative position of the equilibrium pointsIn the abscissa the three equilibrium points lie in the interval*$]C, 1[$. *Therefore, the equation* $p(u) = 0$ *has three positive real roots* u_1, u_2 *and* u_3. *Moreover,*

(a) $C < u_2 < u_3 < 1$
(b) *We have* $u_1 < u_2 < u_3$, *or* $u_2 < u_1 < u_3$, *or* $u_2 < u_3 < u_1$.

We define the following subregions within the parameter space:

$$\Lambda_1 = \left\{(E, C) \in \Lambda / E\frac{1 - 2E}{2 - 3E} < C < E\frac{1 - E}{3E + 1} \text{ and } E < \frac{1}{3}\right\}$$

$$\Lambda_2 = \left\{(E, C) \in \Lambda / E\frac{1 - 2E}{2 - 3E} < C < E\frac{1 - E}{3E + 1} \text{ and } E > \frac{1}{3}\right\}$$

where $\Lambda = \left\{(E, C) \in \left(\mathbb{R}_0^+\right)^2 / 0 < C < E\frac{1-E}{3E+1}\right\}$

Then, for the equilibria at the interior of the first quadrant, we have

(A) $u_1 < u_2 < u_3$, if $(E, C) \in \Lambda_1$.
(B) $u_2 < u_1 < u_3$, if $(E, C) \in \Lambda - (\Lambda_1 \cup \Lambda_2)$
(C) $u_2 < u_3 < u_1$, if $(E, C) \in \Lambda_2$.

In Fig. 2 we display these conditions.

Since the three equilibrium points lie at the nullclines $1 - u - (1 - Nv)v = 0$ and $u(1 - Nv) - C = 0$, then the Jacobian matrix can be written as

$$D\tilde{Z}_\lambda(u, v) = \begin{pmatrix} -u & (2Nv - 1)u \\ B(1 - u) & -BNuv \end{pmatrix}$$

From the predator nullcline we have that $v = \frac{u-C}{uN}$. Then, for any of the equilibrium point at the interior of the first quadrant we have:

$$D\tilde{Z}_{\lambda}(u,v) = \begin{pmatrix} -u & u-2C \\ B(1-u) & -B(u-C) \end{pmatrix},$$

Therefore,

$$\det D\tilde{Z}_{\lambda}(u,v) = B(2u^2 - (3C+1)u + 2C),$$

and

$$\mathrm{tr} D\tilde{Z}_{\lambda}(u,v) = -u - B(u-C) < 0.$$

Then, the nature of these equilibrium points depends only on the determinant of its Jacobian matrix.

Theorem 9. *Nature of the equilibrium point* $\left(E, \frac{(1-E)E}{C}\right)$

(a) *If* $\nabla = 2E^2 - 3EC + 2C - E > 0$, *or,* $C < E\frac{2E-1}{3E-2}$, *the point* $\left(E, \frac{(1-E)E}{C}\right)$ *is a local attractor and the order* $u_1 < u_2 < u_3$ *or* $u_2 < u_3 < u_1$ *holds.*

(b) *If* $\nabla = 2E^2 - 3EC + 2C - E < 0$, *the point* $\left(E, \frac{(1-E)E}{C}\right)$ *is a saddle point and the order* $u_2 < u_1 < u_3$ *holds (Fig. A.4).*

Theorem 10. *Nature of equilibrium points* (u_2, v_2) *and* (u_3, v_3).

(a) *If* $\nabla = 2E^2 - 3EC + 2C - E > 0$, *the order* $u_1 < u_2 < u_3$ *or* $u_2 < u_3 < u_1$ *holds.*
  - *If the order is* $u_1 < u_2 < u_3$, *the point* (u_2, v_2) *is a saddle point and* (u_3, v_3) *is a local attractor.*
  - *If the order is* $u_2 < u_3 < u_1$, *the point* (u_3, v_3) *is a saddle point and* (u_2, v_2) *is a local attractor.*

(b) *If* $\nabla = 2E^2 - 3EC + 2C - E < 0$, *both points* (u_2, v_2) *and* (u_3, v_3) *are local attractors.*

4. Discussion

The development of ecological theory has been catalyzed by the use of mathematical models of living systems. In studying ecological models, it is often preferable to adopt a mixed strategy of mathematical analysis of simple theoretical models and numerical analysis of more realistic and complex models. Realistic models, often composed of many state variables, nonlinear functional relationships and a large number of parameters, are virtually impossible to study by analytical methods and thus we are forced to use numerical approximations via computer simulations. Although the numerical approach strategy gives valuable insights on the functioning of ecological systems, major drawbacks arise since (a) nonlinearity often generates a high sensitivity of solutions to variation in parameter values, and (b) most often, we lack information about true parameter values. This imply that the obtained conclusions might be highly biased by the particular choice we made about the set of parameter values and the exact form of functional relationships. Analytical approaches are exact and general, but limited to very simple models. However, the formal analysis of even the most simple model provides the skeleton of theories and a main source of specific hypotheses to be tested by numerical simulations.

In this study we present an analytical examination of a predator-prey model incorporating inducible defenses. Our goal was to contribute to the development of a comprehensive theory of food web dynamics that considers prey reactions to predator risk. Mathematically, our study system belongs to the Kolmogorov type models (Freedman, 1980), in which the coordinate axes are invariant sets. Also, the model obeys mass-action (Berryman et al., 1995) and biomass conversion (Ramos-Jiliberto, 2005) principles.

We verified that for any set of parameter values the equilibrium points (0, 0) and (K, 0) of our model are saddle points, which implies that both populations always coexist. Moreover, there is a wide range of parameter values for which the system has a unique positive equilibrium point (see Lemma 5) being this globally asymptotically stable (see Theorem 6). Other, more complex system behaviors are discussed below.

4.1. Alternative stable states

The dynamics of system (2) are quite different from other simple models that incorporate prey defenses. In particular, our study system could simultaneously present, under certain circumstances determined by parameter values, two feasible stable points at which (positive) population trajectories could end. Our analysis revealed the existence of a region within the parameter space for which three positive equilibrium points coexist (see Lemma 5). In this case (see Theorems 9 and 10), two equilibrium points are attractors (locally asymptotically stable points) and a third one is a saddle point, which is a type of unstable equilibrium point that exhibits a stable (attracting) and an unstable (repelling) manifold in the state-variable space. A curve appeared in the phase plane, called separatrix, determined by the stable manifold of the saddle point, that splits the state-variable space into two basins of attraction. Each basin defines a subset of population trajectories which tend to reach a given attractor.

When there is a single feasible equilibrium point in the system, the properties of the studied model coincide with those obtained in Almanza-Vásquez et al. (2012), where the fraction of the prey population using refuges is described by a prey-dependent saturated function.

The existence of two attracting equilibrium points is an interesting property of this analyzed model, since a simple and widely observed mode of prey defenses was shown able to generate alternative stable states (Scheffer et al., 1993; Folke et al., 2004; Knowlton, 2004). Given that multiple basins of attraction exist in some systems such as the one studied here, strong enough displacements from a stable state could lead the state variables to reach a different stable state. This phenomenon is known as phase shift and constitutes an explanation to abrupt shifts in ecological conditions, such as the change form clear to turbid waters in shallow lakes, changes in vegetation cover or pest outbreaks (see Schröder et al., 2005 for a review of empirical evidence).

4.2. Refuges, prey defenses and system stability

It has become common among ecologists to affirm that the use of refuges by a fraction of the prey population exerts a stabilizing effect. This is more commonly found when predator–prey interactions are represented by deterministic continuous time models (Sih, 1987). This assertion has been verified in a Lotka–Volterra model described by a nonlinear ordinary differential system, by considering the abundance of hidden prey x_r is a fixed quantity $x_r = \delta$ (González-Olivares and Ramos-Jiliberto, 2012; Harrison, 1979; Ma and Wang, 2015; Maynard Smith, 1974; Taylor, 1984) or, in our conceptual frame (Table 1) when the average prey vulnerability to predators decreases with prey density. This result can also be extended when the prey population exhibits a self-regulated growth, i.e. the prey growth rate described by the logistic equation. In such cases there is a single positive equilibrium point, which is globally asymptotically stable (Collings, 1995; lez-Olivares and Ramos-Jiliberto, 2003, 2004; González-Olivares and Ramos-Jiliberto, 2004), property that can be proven by constructing a Lyapunov function (Goh, 1980). An important consequence of this kind of defensive responses is that the equilibrium population size of prey is increased while the predator population size is decreased (González-Olivares and Ramos-Jiliberto, 2004, 2012; Ma et al., 2009a, 2009b). Another common way to study the effects of defensive responses on predator–prey dynamics has been considering that a variable amount of prey, directly proportional to prey population size, protects from predation via exploiting physical refuges (Yang and Zhang, 2016). This is equivalent to consider that prey exhibit some constant level of immunity to predation, $R=\delta$, which describes what is known as constitutive defenses. By incorporating this function on any Gause-type model (Freedman, 1980), the new system has the same properties of the original. This is proven in González-Olivares and Ramos-Jiliberto, 2003 (see Theorem 1), where it is shown that the only change obtained in the dynamics of the system is a reduction of the carrying capacity K, without altering the stability properties of equilibria. The general conclusions from these studies is that incorporating prey defenses in form of refuges that protect a constant number of prey, or equivalently prey immunity that decreases with prey density, leads to a stronger stabilizing effect on population dynamics, compared to refuges protecting a constant proportion of prey, or equivalently a constant average prey vulnerability (Srinivasu and Gayitri, 2005).

In Collings, 1995; lez-Olivares and Ramos-Jiliberto (2004) Collings, 1995, it is shown that the interpretation of the stabilizing role of prey defenses can not be assumed to be general since for more complex models the use of refuges can exert a locally destabilizing effect, due to the emergence of stable limit cycles that define an oscillatory behavior of populations (Srinivasu and Gayitri, 2005). Other predator–prey models that incorporate antipredator defenses have been analytically studied in McNair (1986). On the other hand, Haque et al. (2014) present a model assuming that average prey immunity is directly related to predator abundance, but also inversely related to prey abundance. A similar model was partially studied in González-Olivares and Ramos-Jiliberto (2004). Haque et al. (2014) showed the existence of conditions in terms of parameter values for which there are three interior equilibria, being two of them locally asymptotically stable points and the third one a saddle point, similar to what we found in this study for a markedly different model of prey defense. In addition, McNair (1986) presented a study of systems with more complex interactions incorporating prey defenses, which were analyzed in Hausrath (1994), thus proving the existence of a unique stable limit cycle (Chicone, 2006).

The model we studied here exhibits a novel behavior, as compared to defense modes analyzed in the bulk of previous studies. Remarkably, incorporating inducible defenses in its most simple way into the Lotka–Volterra model with logistic prey growth, drives an asymptotic behavior that is more diverse than previously thought. Particularly, depending on parameter values, the system (3) and its equivalent form (5) will exhibit either one or two stable states. In the case of exhibiting two alternative stable states, the population trajectories of both prey and predators approach either a low or a high final state, in dependence on initial conditions and stochastic forces that could shift the trajectories to another basin of attraction. Finally, it can be demonstrated (see Proof of Theorem 6 in Appendix A) that no oscillatory attractors exist in the studied system, at least for biologically feasible (i.e. positive) values of the state variables.

4.3. Final remarks

Most known species have developed a wide array of strategies to face predation in order to maximize fitness. Here we present a simple framework that classifies antipredator strategies into six major forms, according to the driving variables that determine immunity of prey to predators (Table 1). Nevertheless, the vast majority of theoretical studies have only considered two of these major types of defenses: constant average immunity (Chen et al., 2012; Devi, 2012, 2013; Ma et al., 2009a, 2009b, 2013; Sarwardi et al., 2012; Wang and Wang, 2012; Wang and Ma, 2014) and average immunity decreasing with prey density (Chen et al., 2009; Devi, 2013; Ji and Wu, 2010; Li et al., 2017; Tao et al., 2011; Tang et al., 2014; Yang and Zhang, 2016). A third case, the one of risk-induced defenses (Table 1) has been studied in a much lesser extent. In this study we analyze the case where average prey immunity to predators is directly related to predator density. This is the most simple way to model inducible defenses, an antipredator strategy that is known to be widespread on earth (Tollrian and Harvell, 1999). Inducible defenses are a form of behavioral flexibility or phenotypic plasticity, which provides the advantage of activating the defense mechanisms (e.g. refuge use, spine development, etc.) only when predation risk is perceived by prey. Nevertheless, the ability to activate and deactivate defenses in response to predation risk is costly, and therefore this strategy is evolutionary favored only in variable or unpredictable environments (Tollrian and Harvell, 1999). Although inducible defenses has been studied numerically in more sophisticated models (Ramos-Jiliberto, 2003; Vos et al., 2004; Ramos-Jiliberto et al., 2007, 2008a, 2008b), fully analytical studies are scarce. Such mathematical work is necessary for strengthen the ecological theory of food web interactions. Next steps in this vein should include the mathematical analysis of the two types of defenses that, to our knowledge, have not been evaluated in the context of predator-prey models: those in which average prey immunity increases with its own population density (see Table 1). Other challenges for future research include improving the biological realism of the studied models by incorporating fitness costs of defenses for the prey, interactions between predation risk and other sources of stress (Heine-Fuster et al., 2017) and further progress in multispecies contexts (Ramos-Jiliberto and Garay-Narvaez, 2007; Garay-Narvaez and Ramos-Jiliberto, 2009).

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Appendix A.

Here, the main properties of the study model are demonstrated.

Proof of Proposition 1. Using the change of variables and time rescaling given by the function

$$\varphi : \mathbb{R}_+^2 \times \mathbb{R} \to \mathbb{R}_+^2 \times \mathbb{R},$$

such that

$$\varphi(u, v, \tau) = \left(K\,u, \frac{r}{q}v, r\tau\right) = (x, y, t);$$

then, we obtain the new system

$$U_\mu : \begin{cases} \dfrac{du}{dt} &= r\left((1-u) - \left(1 - \delta\dfrac{r}{q}v\right)v\right)u \\ \dfrac{dv}{dt} &= \left(pKu\left(1 - \delta\dfrac{r}{q}v\right) - c\right)v. \end{cases}$$

$$Z_\mu : \begin{cases} \dfrac{du}{d\tau} &= \left(1 - u - (1 - \delta\dfrac{r}{q}v)v\right)u \\ \dfrac{dv}{d\tau} &= \dfrac{pK}{r}\left(u\left(1 - \delta\dfrac{r}{q}v\right) - \dfrac{c}{pK}\right)v. \end{cases}$$

Proof of Lemma 3. (a) If $u = 1$, then $\frac{du}{d\tau} = -(1-Nv)v < 0$, for $1 - Nv > 0$,for any sign of $\frac{dv}{d\tau}$.

If $v = \frac{1}{N}$, then $\frac{dv}{d\tau} < 0$, and the trajectories cross to interior $\overline{\Gamma}$.

Moreover, the axes $u = 0$ and $v = 0$, are invariant sets. Then, the set $\overline{\Gamma}$ is an invariant region.

(b) We define the new function

$$w(\tau) = u(\tau) + \frac{1}{S}v(\tau).$$

The time derivative of w along a solution of system (5) is

$$\frac{dw}{d\tau} = \frac{du}{d\tau} + \frac{1}{S}\frac{dv}{d\tau} = ((1-u)(u-M) - Qv)u^2 + (u-v)v.$$

Now,

$$\frac{dw}{d\tau} + \alpha w = ((1-u)(u-M) - Qv)u^2 + (u-v)v + \alpha\left(u + \frac{1}{S}v\right) = H$$

with α being a parameter to be determined.

The right hand side of the above relation can be written as:

$$H = \frac{v\alpha - Bu^2 + Bu + Bu\alpha - BCv}{B}$$

Let $\alpha = BC$; thus,

$$H = (BC+1)u - u^2 = -\left(u - \frac{(BC+1)}{2}\right)^2 + \frac{(BC+1)^2}{4}.$$

so,

$$\frac{dw}{d\tau} + BCw \le \frac{(BC+1)^2}{4}.$$

Let $\delta = \frac{(BC+1)^2}{4}$. Thus, there exists $\delta > 0$, such that

$$0 \le \frac{dw}{d\tau} + BCw \le \delta,$$

being a first order linear inequality.

Applying the theorem on differential inequality (Birkhoff and Rota, 1982), we obtain

$$w(u,v) \le \frac{\delta}{BC} + \left(w(u(0), v(0)) - \frac{\delta}{BC}\right) \qquad \exp \quad (-BC\tau).$$

Clearly, when $\tau \to \infty$, then $0 \le w(u,v) \le \frac{\delta}{BC}$, and the solutions of system (5) are bounded.

Moreover, there exists a set

$$B = \left\{(u,v) \in \overline{\Omega} / w(u,v) \le \frac{\delta}{BC} + \varepsilon,\ \forall \varepsilon > 0\right\}$$

where B is the region in which all the solutions of system (5) that start in $\overline{\Omega}$ are confined. □

We note that the region $\overline{\Gamma}$ is compact.

Proof of Lemma 4. (a) Evaluating the Jacobian matrix at (0, 0) we have that

$$DZ_\eta(0,0) = \begin{pmatrix} 1 & 0 \\ 0 & -BC \end{pmatrix}$$

$$DZ_\eta(1,0) = \begin{pmatrix} -1 & -1 \\ 0 & B(1-C) \end{pmatrix}$$

with $\det DZ_\eta(1,0) = -B(1-C) < 0$ and $(1, 0)$ being a saddle point. □

Proof of Lemma 5. Using the quotient between $p(u)$ and the binomial $u - E$, i.e.,

$$\frac{Nu^3 - Nu^2 + Cu - C^2}{u - E} = Nu^2 + (-N + EN)u + C - EN + E^2N + \frac{NE^3 - NE^2 + CE - C^2}{u - E}$$

we obtain

$$NE^3 - NE^2 + CE - C^2 = 0,$$

that is, $N = C\frac{E-C}{E^2(1-E)}$, with $C < E < 1$.

$$Nu^2 - N(1-E)u + C - EN + E^2N = 0.$$

$$(E-C)u^2 - (1-E)(E-C)u + EC(1-E) = 0,$$

whose solutions are

$$u_2 = \frac{1}{2(E-C)}\left((1-E)(E-C) - \sqrt{W}\right),$$

$$u_3 = \frac{1}{2(E-C)}\left((1-E)(E-C) + \sqrt{W}\right),$$

with $W = (1-E)(E-C)\left(-3EC - C - E^2 + E\right)$.

$$D = -3EC - C - E^2 + E,$$

that is, $C = \frac{E(1-E)}{3E+1}$ is a bifurcation curve in the parameter space. □

Proof of Theorem 6. Let $u = E$ be; then, we have that $v = \frac{(1-E)E}{C}$ and the Jacobian matrix of (5) is

$$D\tilde{Z}_\lambda\left(E, \frac{(1-E)E}{C}\right) = \begin{pmatrix} -E & -2C + E \\ B(1-E) & -B(E-C) \end{pmatrix},$$

and

$$\det D\tilde{Z}_\lambda\left(E, \frac{(1-E)E}{C}\right) = B\left(2E^2 - 3EC + 2C - E\right).$$

$$\nabla = 2E^2 - 3E\left(E\frac{1-E}{3E+1}\right) + 2E\frac{1-E}{3E+1} - E = E\frac{(3E-1)^2}{3E+1} > 0$$

$$\mathrm{tr} D\tilde{Z}_\lambda\left(E, \frac{(1-E)E}{C}\right) = -E - B(E-C) < 0$$

and the point $\left(E, \frac{(1-E)E}{C}\right)$ is an attractor.

$$Z_\eta : \begin{cases} \dfrac{du}{d\tau} = \left((1-u) - (1-Nv)v\right)u & = P(u,v) \\ \dfrac{dv}{d\tau} = B\left(u(1-Nv) - C\right)v & = G(u,v) \end{cases},$$

$$\frac{\partial(PG)}{\partial u} + \frac{\partial(QG)}{\partial u} = -\frac{1}{v} - BN < 0.$$

Proof of Theorem 7. (a) The Jacobian matrix is

$$D\tilde{Z}_\lambda(E, 3E+1) = \begin{pmatrix} -E & \dfrac{(5E-1)E}{3E+1} \\ B(1-E) & -\dfrac{4E^2B}{3E+1} \end{pmatrix},$$

obtaining that

$$\det D\tilde{Z}_\lambda(E, 3E+1) = \frac{EB(3E-1)^2}{3E+1} > 0,$$

and

$$\operatorname{tr}(E, 3E+1) = -E - 4B\frac{E^2}{3E+1} < 0$$

for which the point $(E, 3E+1)$ is an attractor.

$$D\tilde{Z}_\lambda\left(\frac{1-E}{2}, \frac{(E+1)(3E+1)}{4E}\right) = \begin{pmatrix} -\frac{1}{2}(1-E) & \frac{1}{2}\frac{(1-E)^2}{3E+1} \\ \frac{1}{2}B(1+E) & -\frac{1}{2}B\frac{1-E^2}{3E+1} \end{pmatrix},$$

obtaining that

$$\det D\tilde{Z}_\lambda\left(\frac{1-E}{2}, \frac{(E+1)(3E+1)}{4E}\right) = 0,$$

and

$$\operatorname{tr} D\tilde{Z}_\lambda\left(\frac{1-E}{2}, \frac{(E+1)(3E+1)}{4E}\right) = -\frac{1}{2}\left(1 - E + B\frac{1-E^2}{3E+1}\right) < 0.$$

Proof of Theorem 8. (a1) Clearly $u_2 < u_3$.(a2) Considering the difference $u_2 - C$ we have

$$u_2 - C = \frac{1}{2(E-C)}\left((1-E-2C)(E-C) - \sqrt{W}\right)$$

which is dependent on the numerator

$$F = (1-E-2C)(E-C) - \sqrt{W}$$

$$(1-E-2C)(E-C) > \sqrt{(1-E)(E-C)\left(-3EC - C - E^2 + E\right)}$$

which is fulfilled if $1-E-2C>0$ or $C < \frac{1-E}{2}$.

$$((1-E-2C)(E-C))^2 - (1-E)(E-C)\left(-3EC - C - E^2 + E\right) > 0$$

or,

$$4C^2(1-C)(E-C) > 0,$$

which is always true for $C<E<1$.

$$\begin{aligned} D &= -3EC - C - E^2 + E = -3E\left(\frac{1-E}{2}\right) - \left(\frac{1-E}{2}\right) - E^2 + E \\ &= -\frac{1}{2}(1-E)(E+1) < 0; \end{aligned}$$

therefore, u_2 is not a real number; then, $u_2 > C$.

$$u_3 - 1 = \frac{1}{2(E-C)}\left(\sqrt{W} - (1+E)(E-C)\right)$$

$$G = \sqrt{W} - (1+E)(E-C) < 0$$

or,

$$(1-E)\left(-3EC - C - E^2 + E\right) - (1+E)^2(E-C) < 0$$

or,

$$-4E^2(1-C) < 0$$

which is always true for $C<E<1$

$$-4E^2(1-C) > 0$$

is obtained; then, $u_3 < 1$

$$u_1 - u_3 = \frac{1}{2(E-C)}\left((3E-1)(E-C) - \sqrt{W}\right).$$

$$\nabla = 2E^2 - 3EC + 2C - E,$$

a new bifurcation curve. Clearly, if ∇=0, we have $C = \frac{E(2E-1)}{3E-2}$.

$$u_1 - u_2 = \frac{1}{2(E-C)}\left((3E-1)(E-C) + \sqrt{W}\right),$$

we also obtain that the relative position of equilibrium points depend on the quantity ∇. □

Proof of Theorem 9. From Theorem 6 we have

$$\det D\tilde{Z}_\lambda\left(E, \frac{(1-E)E}{C}\right) = B\left(2E^2 - 3EC + 2C - E\right)$$

then, the behavior of this equilibrium point is dependent on the quantity

$$\nabla = 2E^2 - 3EC + 2C - E.$$

□

Proof of Theorem 10. Considering Theorem 8 about the nature of equilibrium point $\left(E, \frac{(1-E)E}{C}\right)$ and because $\operatorname{tr} D\tilde{Z}_\lambda(u, v) = -u - B(u-C) < 0$. □

Appendix B.

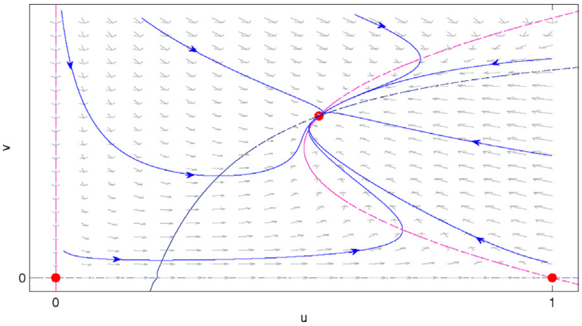

Fig. A.1. For $B=1$, $C=0.2$ and $E=0.5$, the unique interior equilibrium point $\left(E, \frac{(1-E)E}{C}\right)$ is globally asymptotically stable.

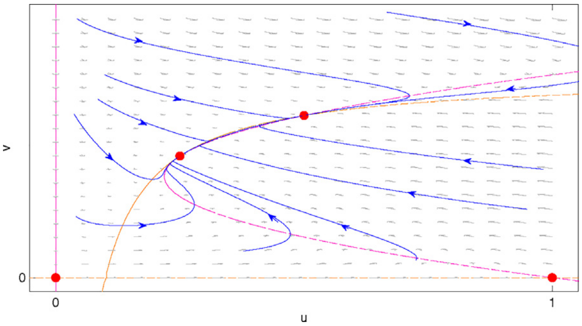

Fig. A.2. For $B=1$, $C=0, 1$ and $E=0, 2$, there exists two interior equilibrium points, one of them being a non-hyperbolic saddle point and the other an attractor (stable) point.

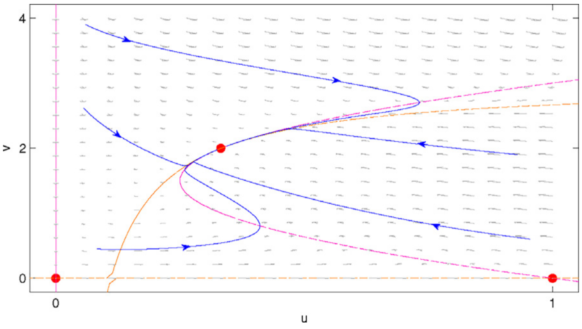

Fig. A.3. For $B = 1$, the particular case in which the three equilibrium points collapse into the non-hyperbolic attractor $(\frac{1}{3}, 2)$.

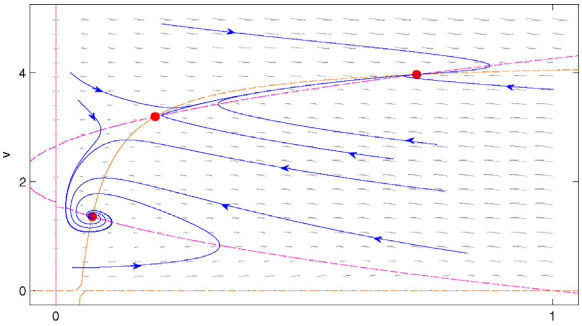

Fig. A.4. Case $u_2 < u_1 < u_3$. Existence of three interior equilibrium points, one of them being a hyperbolic saddle point whose stable manifold splits the behavior of the trajectories. The two other points are a focus attractor and a node attractor. Parameter values are $B = 1$, $C = 0.05$ and $E = 0.2$.

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