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Dynamic consequences of prey refuges in a simple model system: more prey, fewer predators and enhanced stability

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Abstract

In this work, we use an analytical approach to study the dynamic consequences of the simplest forms of refuge use by the prey. Although this problem is not new, there are surprisingly few intents to clarify the role of prey refuges in simple predator–prey models other than the original Lotka–Volterra equations. Here we incorporate prey refuges in a widely known continuous model that satisfies the principle of biomass conversion. We will evaluate the effects with regard to the local stability of equilibrium points in the first quadrant, equilibrium density values, and the long-term persistence of the populations.

We show that there is a trend from limit cycles through non-zero stable points up to predator extinction and prey stabilizing at high densities. This transitions occur as hidden prey increase in number or proportion, and/or increases the ratio of mortality to conversion efficiency of predators. The domains of stability in terms of the parameter space differ between the two modes of refuge use analyzed.

Keywords: Stability; Limit cycles; Bifurcation; Predator–prey models; Refuge

1. Introduction

The study of the consequences of individual behavior on the population phenomena can be recognized as a major issue in contemporary theoretical ecology. Nevertheless, linking behavior to population dynamics has received comparatively little attention (Real and Levin, 1991).

In the frame of predator–prey systems, most of the empirical and theoretical work has considered the behavior of predators and its implications on the population dynamics (Harrison, 1979; Holling, 1959; Murdoch and Oaten, 1975; Ruxton, 1995; Sih et al., 1988). At a comparatively smaller extent, the hiding behavior of preys has been incorporated as a new ingredient of simple predator–prey models and its major consequences on the system stability have been studied. This was initially done by modifying the original Lotka–Volterra predator–prey equations and the most widely reported conclusion was the community equilibrium being stabilized by the addition of refuges for preys, and prey extinction being prevented (Harrison, 1979; Holling, 1959; Maynard Smith, 1974; Murdoch and Oaten, 1975; Sih, 1987).

The traditional ways in which the effect of refuge use by the preys has been incorporated in predator–prey models is to consider either a constant number or a constant proportion of the prey population being protected from predation (Taylor, 1984).

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The effect itself of refuge use (and probably of any antipredator strategy) on the population growth is complex in nature, but for modeling purposes it can be understood as constituted by two components: the first one is a primary effect, comprising the reduction of prey mortality due to reduction in predation success. Therefore, primary effects affect positively the population growth of preys and negatively that of predators. Secondary effects could include trade-offs and by-products of the prey behavior that could be either advantageous or detrimental for the involved populations. A classic secondary effect is the reduction in prey's birth rate due to the sub-optimal states of resources and/or conditions in the refuge. Furthermore, a different kind of effects—indirect effects—could arise in more complex food-web models as a result of the feedback structure of the system.

More complex models incorporating prey refuges have been introduced and analyzed by McNair (1986), Sih (1987), Ruxton (1995), and Scheffer and de Boer (1995), among others, which implicitly assume the existence of cost on the prey growth rate, and other secondary effects such as predator dependence of refuge use. The conclusions commonly are referred to as changes in the stability properties of the system explained by the addition of refuge. Nevertheless, the results are often ambiguous and difficult to interpret in biological terms.

An accepted strategy is to study the most simple but plausible models before to move toward more complex ones if empirical or theoretical evidence justifies this. On the basis of the Lotka–Volterra formulation, more realism has been added to obtain simple predator–prey models, through including self-limitation in the lowest-level population, and by making saturating the functional and numerical responses (May, 1974). Nevertheless, to our knowledge there are surprisingly few studies in which the primary effect of refuge is incorporated into simple continuous predator–prey models other than the original Lotka–Volterra.

An exception is the work of Collings (1995), which introduces and analyzes a model, attributed to May (1973) in its original form, where the population growth of both preys and predators is logistic in absence of predation, and the functional response is hyperbolic. They incorporate the refuge as a constant fraction of the prey, by which the predator carrying capacity and the prey mortality due to predation are affected. The logistic model used by Collings belongs to a family that do not conform to the principle of biomass conversion. That is, the functional and numerical responses are not explicitly related. The model we will use here to incorporate the primary refuge effect, on the other hand, is a natural extension of the Lotka–Volterra model with the inclusion of prey self-limitation and a Holling II functional response. Here the predator reproductive rate responds only to the rate of prey killed per predator, thus obeying the principle of biomass conversion (Ginzburg, 1988). This model has a long tradition in theoretical ecology (Ginzburg, 1988; May, 1974; Maynard Smith, 1974; Murray, 1989; Yodzis, 1989) and a systematic study of the effects of prey behavior on the system dynamics should not disregard its use as a starting point.

Recognizing that there is a huge variety of predator–prey models in the ecological literature, those best known and understood in mathematical and biological terms are likely to be the Lotka–Volterra model, the May model, and the Rosenzweig–MacArthur model (Rosenzweig, 1971) which we use here. As mentioned above, the theoretical study of the population consequences of prey's refuge in its simplest form has been done on the first two only and this work intends to fill this gap.

For consistency with the previous works on this field, we will consider refuge as an environmental place where predation rate is lower. Likewise, we will consider, as usual, the effect of having a constant number of prey and a constant proportion of preys using refuges. The mathematical analysis will be done separately in each case.

We will evaluate the effects of refuge use by the prey, through the analysis of the following model responses: (a) local stability of equilibrium points in the first quadrant, (b) equilibrium density values, and (c) long-term persistence of each population.

2. The basic model

We assume the populations sizes changing continuously with time, uniform distribution over space and neither age or sex structure. The model, we will analyze here belong to the general Gause model (Freedman, 1980), which is represented by the second-order differential equations system:

$$X:\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t}=xg(x)-y\phi(x)\\[2mm]\dfrac{\mathrm{d}y}{\mathrm{d}t}=(p\phi(x)-c)y\end{cases}\tag{1}$$

We denote by $x = x(t)$ the population size of prey (measured in biomass or number density), and by $y = y(t)$ the population size of predators. The following assumptions are implicit in this model (Hasík, 2000):

(i) There exists a number $K > 0$ such that $g(x) > 0$ for $0 < x < K$; $g(K) = 0$; $g(x) < 0$ for $x > K$.
(ii) $\phi(0) = 0$; $\phi'(x) > 0$ for $x > 0$; $\phi'_{+}(0) > 0$.
(iii) There is a unique point $(x_{\mathrm{e}}, y_{\mathrm{e}})$ with $0 < x_{\mathrm{e}} < K$, $y_{\mathrm{e}} > 0$ such that $p\phi(x_{\mathrm{e}}) - c = 0$ and $x_{\mathrm{e}}g(x_{\mathrm{e}}) - y_{\mathrm{e}}\phi(x_{\mathrm{e}}) = 0$.
(iv) The prey isocline $h(x) := xg(x)/\phi(x)$ is a strict concave down function, symmetric with respect to its maximum which is attained at a point $m > 0$.
(v) The functions $g(x)$ and $\phi(x)$ are smooth as required.

According to Maynard Smith (1974), there exists a quantity x_r of the prey population that occupies a refuge. This quantity is considered from two alternative points of view: (a) the quantity of hidden prey is proportional to the size of the prey population at instant t, i.e. $x_r = \beta x$ or else, (b) the quantity of hidden prey is a constant $x_r = \gamma$, i.e. the quantity of refuged prey depends on the capacity of hiding places found in the environment.

In the first case, the dynamics of the model with proportional refuge, given a logistic growth function of the prey, is equivalent to the dynamics of the original model:

Theorem 1. *The effect of refuge utilization by a constant fraction of the prey population, i.e. with $x_r = \beta x$, on a system represented by a Gause type model of the form*

$$X:\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t}=r\left(1-\dfrac{x}{K}\right)x-y\phi(x)\\[2mm]\dfrac{\mathrm{d}y}{\mathrm{d}t}=(p\phi(x)-c)y\end{cases}$$

is equivalent to reduce K (the environmental carrying capacity) by a proportion $1-\beta$.

We note that the vector field Y^{β} of Appendix A accounts for the dynamics of prey $x_{(n)}(t)$. The only difference between the vector field X^{β} and Y^{β} is the decrease of the carrying capacity by $1-\beta$, determining a new value for x_{e} and y_{e}.

Corollary 2. *The dynamics of the vector field Y^{β} related to exposed prey $x_{(n)}(t) = (1-\beta)x_{(o)}$ is the same of that of vector field X^{β}.*

We will analyze in more detail the effect of adding prey refuges to a specific predator–prey system represented by the well-known Rosenzweig–MacArthur model (see Rosenzweig, 1971; May, 1974; Murray, 1989; Yodzis, 1989):

$$X_{\mu}:\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t}=r\left(1-\dfrac{x}{K}\right)x-\dfrac{qxy}{x+a}\\[2mm]\dfrac{\mathrm{d}y}{\mathrm{d}t}=b\left(\dfrac{px}{x+a}-c\right)y\end{cases}\tag{2}$$

where $\mu = (r, K, q, a, b, c, p) \in \Re^{7}_{+}$, and the parameters having the following biological meanings: r is the intrinsic per capita growth rate of prey; K is the prey environmental carrying capacity; q is the maximal per capita consumption rate of predators; a is the amount of prey needed to achieve one-half of q; c is the per capita death rate of predators; and p is the efficiency with which predators convert consumed prey into new predators.

In Berryman et al. (1995), the vector field X_{μ} with $b = 1$ is classified as a “prey-dependent functional response model”. The function $h(x) = (qx/x + a)$, is a saturating functional response of the kind Holling type II—Michaelis–Menten–Monod and it represents the amount of prey killed per unit time by an individual predator. Note that predators do not exhibit self-interference since $(\partial h/\partial y) = 0$. In this functional response, the parameter a is a measure of the abruptness of the function (Getz, 1996). If $a \to 0$, the curve increases fast whereas if $a \to K$, the curve grows slowly, i.e. a greater quantity of prey is needed to attain $q/2$.

As a bioeconomic model, $y = y(t)$ indicates the fishing effort which is the number of standardized vessels-gear units actively fishing at time t. Parameter q represents catchability, p is the per unit biomass price of the landed fish, c is the fishing cost per unit effort

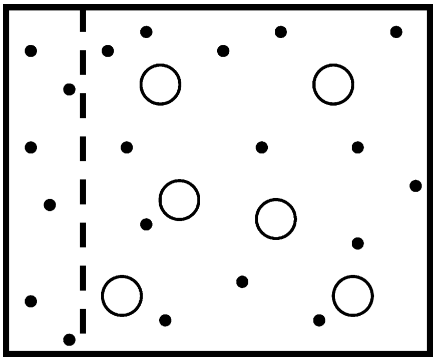

Fig. 1. Conceptual diagram of the Rosenzweig–MacArthur model with prey refuge. Small black circles represent the prey, large circles represent predators. The vertical dashed line represents the boundary of a refuge, where prey are invulnerable to predators. The refuge could protect either a constant number or a constant fraction of the total prey population.

and b is the stiffness parameter that measures the speed with which the effort y reacts in the perceived rent flow (Clark, 1990; Goh, 1980; González-Olivares, 1998).

This predator–prey model has been widely studied in many papers. For instance, in Cheng (1981), Hasík (2000), and Sugie et al. (1997), the uniqueness of the limit cycle is proved; in Cheng et al. (1981) and Sugie and Katayama (1999), it is shown as a necessary and sufficient condition under which the positive equilibrium of (2) is globally asymptotically stable; Sunhong (1989) provides a classification of its global structure; Ardito and Ricciardi (1995) provide Lyapunov functions to prove its global asymptotic stability and Hesaaraki and Moghadas (2001) provide conditions for the existence of limit cycles.

According to Collings (1995), we modified the functional response of the model (2), and obtained the system:

$$X_\mu^{x_r}:\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t}=r\left(1-\dfrac{x}{K}\right)x-\dfrac{q(x-x_r)y}{x-x_r+a}\\[2ex]\dfrac{\mathrm{d}y}{\mathrm{d}t}=b\left(\dfrac{p(x-x_r)}{x-x_r+a}-c\right)y\end{cases}$$

which is graphically represented in Fig. 1.

3. A constant proportion of prey using refuges

When considering $x_r=\beta x$, the model that represent this situation is given by the Kolmogorov type system:

$$X_\mu^{\beta}:\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t}=\left(r\left(1-\dfrac{x}{K}\right)-\dfrac{q(1-\beta)y}{(1-\beta)x+a}\right)x\\[2ex]\dfrac{\mathrm{d}y}{\mathrm{d}t}=b\left(\dfrac{p(1-\beta)x}{(1-\beta)x+a}-c\right)y\end{cases}$$

which can be written as

$$X_\mu^{\beta}:\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}t}=\left(r\left(1-\dfrac{x}{K}\right)-\dfrac{qy}{x+(a/(1-\beta))}\right)x\\[2ex]\dfrac{\mathrm{d}y}{\mathrm{d}t}=b\left(\dfrac{px}{x+(a/(1-\beta))}-c\right)y\end{cases}\qquad(3)$$

that is, the only change relative to system (2) is the new value of the half saturation constant $a'=(a/(1-\beta))$. It is easy to see that the dynamics of the system (3) is topologically equivalent to the original system (Andronov et al., 1973; Sotomayor, 1979). When $\beta\to 0$, the new half saturation constant a' is close to the original one, while if $\beta\to 1$, the value of a' increases.

The equilibrium points of vector field X_μ^{β} are $O=(0,0)$, $P_K=(K,0)$ and $P_\mathrm{e}=(x_\mathrm{e},y_\mathrm{e})$ with $x_\mathrm{e}=(a'c/(p-c))$ and $y_\mathrm{e}=(a'rp(K(p-c)-a'c))/q(p-c)^2$; and clearly if $K(p-c)-a'c=K(p-c)(1-\beta)-ac=0$, the point P_e collapses with P_K.

Following the methodology used in Sáez and González-Olivares (1999), we make a reparameterization of the vector field X_μ^{β} or the system (3) including changes of variables and a time rescaling given by the function $\varphi:(\mathfrak{R}_0^+)^2\times\mathfrak{R}\to(\mathfrak{R}_0^+)^2\times\mathfrak{R}$, such that

$$\varphi(x_{(n)},y_{(n)},\tau)=\left(Kx_{(n)},\frac{rK}{q}y_{(n)},\frac{r}{x+A}\tau\right)=(x_{(o)},y_{(o)},t)$$

Here, the subindex (n) indicates the new variable and (o) the older. We get

$$\det D\varphi(x_{(n)},y_{(n)},\tau)=\frac{r^2K^2}{q(x+A)}>0$$

The vector field in the new coordinates is $Z\eta=\varphi\circ X_\mu^{\chi}$ (Dumortier, 1978), and the associated second-order differential equations system is the following Kolmogorov type polynomial:

$$Z_\mu:\begin{cases}\dfrac{\mathrm{d}x}{\mathrm{d}\tau}=((1-x)(x+A)-y)x\\[2ex]\dfrac{\mathrm{d}y}{\mathrm{d}\tau}=B(x-C(x+A))y\end{cases}\qquad(4)$$

which has only three parameters, i.e. $\mu = (A, B, C) \in \Re^3_+$, where $A = (a'/K)$, $B = (bp/r)$, $C = (c/p)$ with $a' = (a/1 - \beta)$ and the system (4) is topologically equivalent to the system (3). The equilibrium points of vector field Z_μ are $O = (0, 0)$, $Q_1 = (1, 0)$, and $Q_e = ((AC/(1 - C)), (A(1 - C - AC)/(1 - C)^2))$. The point $Q_e \in \Re^2_+$, if and only if $1 - C > 0$ and $N = 1 - C - AC > 0$. If $N = 0$, the points Q_1 and Q_e collapse, and if $N < 0$, the point Q_e lies within the fourth quadrant and Q_1 is globally asymptotically stable.

Theorem 3. *Let* $(A, C) \in \Re^2_+$

- (i) *If* $0 < A < (1 - C)/(1 + C) < 1$, *the system* (4) *has a unique limit cycle surrounding the point* Q_e.
- (ii) *If* $0 < (1-C)/(1+C) < A < ((1-C)/C) < 1$, *the system* (4) *has a unique stable equilibrium point at* Q_e.
- (iii) *If* $0 < ((1 - C)/C) < A < 1$, *the system* (4) *has a stable equilibrium point at* (1, 0) *and* Q_e *is at the fourth quadrant*.

Fig. 2 shows a two-parameter bifurcation diagram where the curves $M = 0$ and $N = 0$ are displayed. That is, $A = (1 - C)/(1 + C)$ and $A = ((1 - C)/C)$, respectively.

We note that parameter B has no importance for this system. In bioeconomic terms, parameter C represents the cost-price relation. In terms of the original parameters we formulate our results as follows:

Theorem 3a. *Let* $(a', c, p, K) \in \Re^4_+$

- (i) *If* $0 < (a'/K) < (p - c)/(p + c) < 1$, *the system* (3) *has a unique limit cycle, surrounding the unique equilibrium point at the first quadrant.*
- (ii) *If* $0 < (p-c)/(p+c) < (a'/K) < ((p-c)/c) < 1$, *the system* (3) *has a unique stable equilibrium point at* $P_e = ((a'c/(p - c)), (a'rp(K(p - c) - a'c)/q(p - c)^2))$.
- (iii) *If* $0 < ((p - c)/c) < (a'/K) < 1$, *the system* (3) *has a stable equilibrium point at (K, 0).*

In reference to parameter β, the former relations can be expressed as:

Theorem 3b. *Let* $(a', c, p, K) \in \Re^4_+$

- (i) *If* $0 < \beta < 1-(a(p+c)/K(p-c))$, *the prey and predator populations oscillate around the unique equilibrium point at the first quadrant.*
- (ii) *If* $0 < 1 - (a(p + c)/K(p - c)) < \beta < 1 - (ac/K(p - c))$, *the populations tend to reach a globally asymptotically stable equilibrium point.*

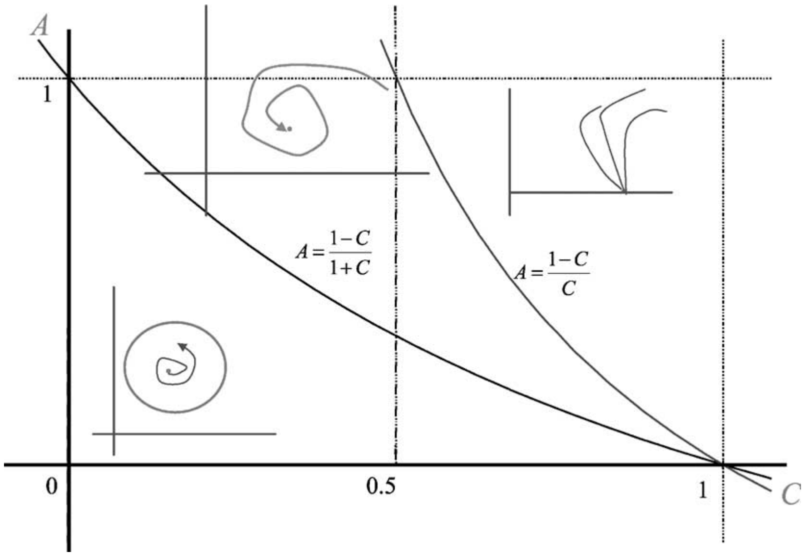

Fig. 2. Bifurcation diagram of system (4), showing the kind of stability inside each domain of attraction.

(iii) *If* $0 < 1 - (ac/K(p-c)) < \beta < 1$, *the prey population tends to reach its maximum value* K *and the predators are depleted.*

4. A constant number of prey using refuges

A different dynamics is expected when a fixed quantity of prey $\gamma > 0$ uses refuges, since the y-axis is not an invariant set. Under this assumption, we get the system

$$X_{\mu}^{\gamma}: \begin{cases} \dfrac{dx}{dt} = r\left(1 - \dfrac{x}{K}\right)x - \dfrac{q(x-\gamma)y}{x-\gamma+a} \\ \dfrac{dy}{dt} = b\left(\dfrac{p(x-\gamma)}{x-\gamma+a} - c\right)y \end{cases} \qquad (5)$$

where the equilibrium points are $O = (0,0)$, $P_K = (K,0)$ and $P_e = (x_e, y_e)$ with $x_e = (ac + (p-c)\gamma/(p-c))$ and $y_e = (pr(ac + (p-c)\gamma)((K-\gamma)(p-c) - ac)/cqK(p-c)^2)$.

Different cases appears, for $\gamma > a$, $\gamma = a$ and $\gamma < a$. If $(K-\gamma)(p-c) - ac = 0$, the point P_e collapses with P_K. We distinguish two cases in this situation: $\gamma \neq a$ and $\gamma = a$. In the first case, we will analyze the model only with $\gamma > a > 0$, since the results are similar when $\gamma < a$.

4.1. Case 1

By considering a fixed quantity of prey occupying refuges, $\gamma > a > 0$, we have four singularities within the first quadrant. Nevertheless, it is of interest only the region defined by $x > \gamma$. Under these circumstances the points $O = (0,0)$ and $P_{\gamma} = (\gamma - a, 0)$ are not considered. As before, in order to simplify the calculus we make a reparameterization using a change of variables and a time rescaling by means of the function φ: $(\Re_0^+)^2 \times \Re \to (\Re_0^+)^2 \times \Re$ given by

$$\varphi(x_{(n)}, y_{(n)}, \tau) = \left(Kx_{(n)}, \frac{rK}{q}y_{(n)}, \frac{r}{x-L+A}\tau\right) = (x_{(o)}, y_{(o)}, t)$$

where the subindex (n) indicates the new variable and (o) the older. We obtain $\det D\varphi(x_{(n)}, y_{(n)}, \tau) = (r^2K^2/q(x-L+A)) > 0$. The vector field in the new coordinates is $Z_{\eta}^{L} = \varphi \circ X_{\mu}^{\gamma}$ (Dumortier, 1978), and the associated differential equation system has only three parameters:

$$Z_{\eta}^{L}: \begin{cases} \dfrac{dx}{d\tau} = (1-x)x(x-L+A) - (x-L)y \\ \dfrac{dy}{d\tau} = B(x - L - C(x-L+A))y \end{cases}$$

with $\eta = (A, B, C) \in \Re_+^3$ for $A = (a/K)$, $B = (bp/r)$, $C = (c/p)$, $L = (\gamma/K)$ and the vector field Z_{η}^{L} is topologically equivalent (Andronov et al., 1973; Sotomayor, 1979) to X_{μ}^{γ}.

We note that the y-axis $(x = 0)$ is not an invariant set of system (6), which corresponds to a second-order polynomial system with one straight invariant line. The equilibrium points of vector field Z_{η}^{L} are $O = (0,0)$, $Q_1 = (1,0)$, $Q_A = (L - A, 0)$ and $Q_e = (x_e, y_e)$ with $x_e = (AC + (1-C)L)/(1-C)$ and $y_e = ((AC + (1+C)L)H)/C(1-C)^2$; where $H(A, C, L) = (1-C)(1-L) - AC$. Only Q_1 and Q_e, are of our interest since $x > L$. We note that the vector field X_{μ}^{γ} is not defined at $x = \gamma - a$, but it is possible to make a continuous extension to the point $(\gamma - a, 0)$. The point Q_e will be in the first quadrant if and only if $1 - C > 0$ and $H > 0$.

Lemma 4.1. *The set* $\Gamma = \{(x,y) \in \Re^2 / L \leq x \leq 1, y \geq 0\}$ *is an invariant region of vector field* Z_{η}^{L}.

Lemma 4.2.

(a) *If* $H > 0$, *the singularity* $(1, 0)$ *of system* (6) *is a saddle point and the singularity* (x_e, y_e) *is found within* Γ.

(b) *If* $H < 0$, *the singularity* $(1, 0)$ *of system* (6) *is a locally stable equilibrium point and the singularity* (x_e, y_e) *is found in the fourth quadrant.*

(c) *If* $H = 0$, *the singularity* (x_e, y_e) *of system* (6) *collapses with the point* $(1, 0)$, *which is a locally stable equilibrium point.*

Theorem 4.3. *Let* $H = (1-C)(1-L) - AC > 0$ *and* $S = (1-C)^3L^2 - (1-C)(2AC^2 + (1-C)^2)L + AC^2(1 - C - AC - A)$

(a) *If* $S > 0$, *the singularity* (x_e, y_e) *of system* (6) *is an unstable equilibrium point, surrounded by a limit cycle.*

(b) *If* $S < 0$, *the singularity* (x_e, y_e) *of system* (6) *is a locally asymptotically stable equilibrium point.*

In terms of the original parameters, the results shown in Appendix A reveal the following propositions:

Lemma 4.1a. *The set* $\Gamma' = \{(x, y) \in \Re^2/\gamma \leq x \leq 1, y \geq 0\}$ *is an invariant region of the vector field* X_η^γ.

Lemma 4.2a. *Let* $H' = (c, p, K, \gamma) = (1 - (\gamma/K))(1 - (c/p)) - (ac/pK)$

(a) *If* $H' > 0$, *the singularity (K, 0) of system* (5) *is a saddle point and the singularity* (x_e, y_e) *is found within* Γ'.

(b) *If* $H' < 0$, *the singularity (K, 0) of system* (5) *is a locally stable equilibrium point and the singularity* (x_e, y_e) *is found in the fourth quadrant.*

Theorem 4.3a. *Let* $H' = (c, p, K, \gamma) = (1 - (\gamma/K))(1-(c/p))-(ac/pK) > 0$ *and* $S'(c, p, K, \gamma) = (p-c)^3\gamma^2 - (p-c)(2ac^2 + K(p-c)^2)\gamma + ac^2(K(p-c) - a(c-p))$

(a) *If* $S' > 0$, *the singularity* (x_e, y_e) *of system* (5) *is an unstable equilibrium point, surrounded by a limit cycle.*

(b) *If* $S' < 0$, *the singularity* (x_e, y_e) *of system* (5) *is a locally asymptotically stable equilibrium point.*

4.2. Case 2

A particular case arises, by considering in system (5) that a fixed quantity $\gamma = a$ of prey occupies refuges. Under this condition, we obtain the system

$$X_\varepsilon^\gamma : \begin{cases} \dfrac{\mathrm{d}x}{\mathrm{d}t} = r\left(1 - \dfrac{x}{K}\right)x - \dfrac{q(x-\gamma)y}{x} \\ \dfrac{\mathrm{d}y}{\mathrm{d}t} = b\left(\dfrac{p(x-\gamma)}{x} - c\right)y \end{cases} \tag{7}$$

where $\varepsilon = (r, K, q, b, c, p) \in \Re_+^6$. By considering $L = A$ in the vector field Z_η^L, we obtain the equivalent system

$$Y_\nu^L : \begin{cases} \dfrac{\mathrm{d}x}{\mathrm{d}\tau} = (1-x)x^2 - (x-L)y \\ \dfrac{\mathrm{d}y}{\mathrm{d}\tau} = B(x(1-C) - L)y \end{cases} \tag{8}$$

where $\nu = (B, C) \in \Re_+^2$ and $x - L > 0$. The equilibrium points are $O = (0, 0)$, $Q_1 = (1, 0)$ and $Q_e = (x_e, y_e)$ where $x_e = (L/(1-C))$ and $y_e = (L(1 - C - L)/C(1-C)^2)$.

The point $Q_e \in \Re_+^2$ if and only if, $1 - C > 0$ and $1 - C - L > 0$. Since $(0, 0) \notin \Gamma$, it will not be analyzed. The Jacobian matrix is now

$$DY_\nu^L(x, y) = \begin{pmatrix} 2x - 3x^2 - y & -(x-L) \\ B(1-C)y & B(x(1-C) - L) \end{pmatrix} \perp$$

It is easily noted that:

(a) If $H = 1 - C - L > 0$, the singularity (1, 0) of system (8) is a saddle point and the singularity (x_e, y_e) is found in Γ.

(b) If $H < 0$, the singularity (1, 0) of system (8) is a locally stable equilibrium point and the singularity (x_e, y_e) is found in the fourth quadrant.

(c) If $H = 0$, the singularity (x_e, y_e) collapses with the singularity (1, 0).

Theorem 5. *In system* (8), *let* $H(C, L) = 1 - C - L > 0$ *and* $S(C, L) = (1 - 3C)L - (1 - C)(1 - 2C)$.

(a) *If* $S > 0$, *the singularity* (x_e, y_e) *is an unstable equilibrium point, surrounded by at least one limit cycle.*

(b) *If* $S < 0$, *the singularity* (x_e, y_e) *is a globally asymptotically stable equilibrium point.*

Fig. 3 presents a two-parameter bifurcation diagram, showing the curves $S = 0$ and $H = 0$, that is, the curves $L = ((1-C)(1-2C))/(1-3C)$ and $L = 1 + C$, respectively. It can be noted that the region of the parameter space for which the singularity (x_e, y_e) is locally stable is larger than the equivalent region in the model without refuge use or with constant proportion refuge.

In terms of the original parameters, we obtain the following:

(a) The set $\Gamma' = \{(x, y) \in \Re^2/\gamma \leq x \leq K, y \geq 0\}$ is an invariant region of vector field X_ε^γ.

(b) If $H''(c, p, K, \gamma) = 1 - (c/p) - (\gamma/K) > 0$, the singularity $(K, 0)$ of system (7) is a saddle point and the singularity (x_e, y_e) is in Γ'.

(c) If $H'' < 0$, the singularity $(K, 0)$ of system (7) is a locally stable equilibrium point and the singularity (x_e, y_e) is in the fourth quadrant.

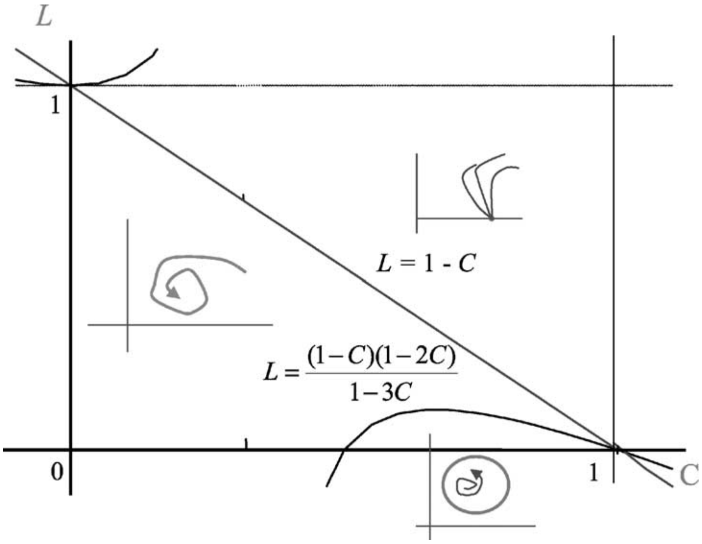

Fig. 3. Diagram of system (8), showing the kind of stability inside each domain of attraction.

(d) If $H'' = 0$, the singularity (x_e, y_e) collapses with the point $(K, 0)$, which is a locally stable equilibrium point.

Theorem 5a. *Let* $H'' > 0$ *and* $S(c, p, K, \gamma) = (p - 3c)p\gamma - K(p - c)(p - 2c)$

(a) *If* $S'' > 0$, *the singularity* (x_e, y_e) *of system* (7) *is an unstable equilibrium point, surrounded by at least one limit cycle.*
(b) *If* $S'' < 0$, *the singularity* (x_e, y_e) *of system* (7) *is a locally asymptotically stable equilibrium point.*

5. Discussion

Earlier theoretical work suggest that the use of refuges by prey has a stabilizing effect on the predator–prey dynamics, particularly when a fixed number of hidden prey is considered (Maynard Smith, 1974; Murdoch and Oaten, 1975; Harrison, 1979; Sih, 1987; Ives and Dobson, 1987; Ruxton, 1995). Nevertheless, other results in the context of different models show no such simple pattern (McNair, 1986; Collings, 1995). On the other hand, it has been shown that refuges could also increase the equilibrium density of prey (Collings, 1995; Ives and Dobson, 1987) or that of both prey and predator (McNair, 1986). In this work, we analyzed the effects of incorporating refuges, as fixed numbers and constant proportion of prey, on the dynamics of the Rosenzweig–MacArthur predator–prey model.

It is important to note that parameter B does not influence the equilibrium and stability properties of the model. This is evident because B does not take part on the determination of the equilibrium point, and it has not influence on the sign of the trace or determinant of the Jacobian matrix evaluated at equilibrium.

Our analyses on the stability properties of the model as a function of the values of the relevant parameters reveals that:

1. Equilibrium density of prey increases while that of predators decreases as refuge use by prey increases and/or predator efficiency decreases. We refer to predator efficiency as the inverse of parameter $C = (c/p)$, which represents the ratio of predator mortality to conversion efficiency. Although several works have shown an increase in prey density as they use refuges (see above), the effect on predator density is less clear. In particular, our results contrast with those of McNair (1986) who predicted an increase in predator equilibrium density with refuge use. Nevertheless, from our results it is easy to show that under a very restricted set of conditions we expect an increase in the equilibrium point of both prey and predators as the proportional

refuge increases. This occurs when the density equilibrium of prey (x_e) is less than $(1 - A)/2$, this point being the maximum of the prey isocline and the point where the stability of the equilibrium changes from repellor to attractor. Therefore, it can be found that predator equilibrium density increases with the proportion of prey refuge, in agreement with McNair's results, only when that equilibrium is unstable and for small values of x_e.

2. When refuge use is high and predator efficiency is low, the models predict that prey reach their carrying capacity and predators go extinct, a behavior also observed by Collings (1995) for certain parameter ranges.
3. The refuge use by prey increases the local stability of the community equilibrium in the first quadrant, which is in agreement with most previous results on simple models, cited above. In this work, stabilization or increase of stability refers to cases where a community equilibrium point changes from repeller to an attractor due to changes in the value of a control parameter (see Edelstein-Keshet, 1988; Strogatz, 1994). Three kind of equilibria can be reached: unstable point with stable orbits, stable coexistence of prey and predators, and predator extinction while the prey reaches its carrying capacity. The parameter conditions under which each of these equilibrium solutions are expected, depend strongly on the mode of refuge use (i.e. constant proportion or constant number of prey).

If a constant proportion of the prey population is using refuges, the stability of equilibria increases with the fraction of hidden prey, and decreases with predator efficiency. Efficient predators in interaction with prey exhibiting low refuge use, results in stable population oscillations (limit cycles). As refuge use increases and/or predator efficiency decreases, the system stabilizes at non-zero densities, and then it stabilizes at the carrying capacity of prey and predator extinction (Fig. 1). Our predictions concerning the increase in prey density and predator extinction agree with the results of Collings (1995) who used a model with a constant proportion refuge, of similar complexity to ours, but founded on different structural assumptions. Our results also agree with those of Scheffer and de Boer (1995), since they found a clear stabilizing effect of prey refuge (fraction of prey not exposed to predators) in their algae-zooplankton model system. Nevertheless, the analyses of McNair (1986) and Collings (1995) show that a stable equilibrium can be transformed to unstable by the addition of constant proportion refuge. The model of McNair (1986) considers costs of refuge use, and the functional response it is not specified. On the other hand, the model of Collings (1995) does not include biomass conversion between prey captured and predator growth. Therefore, the basic assumption implicit in those models are different to ours.

With a constant number of hidden prey, population oscillations can occur only under a very restricted set of parameter values i.e. with very few prey occupying refuges and the predator having a high mortality rate relative to its efficiency to convert killed prey into own tissues. A large portion of the parameter space drives to predator extinction (see Fig. 2). This occur at high levels of refuge use if predator are very efficient, and with smaller number of hidden prey as predator are less efficient. A stable equilibrium can never transform to unstable by the addition or by increasing of constant number refuge, in close agreement with earlier results (Maynard Smith, 1974; McNair, 1986; Sih, 1987).

Our results indicate that efficient predators (with $C < 0.5$) will never go extinct if a constant proportion of prey occupies refuges, but the same efficient predators could disappear if a high constant number of prey occupies refuges. Conversely, inefficient predators can easily go extinct if prey increases the use of refuge, either as a constant proportion or number. The main differences between the two modes of refuges lies in that the constant number refuge model predict a larger space of conditions under which stable non-zero densities as well as predator extinction occur, relative to the predictions of the constant proportion refuge model. Our major results are summarized in Table 1, where it is shown the effects of increasing refuge use under the different models and parameter conditions worked out.

Although our results are valid under some restrictive assumptions derived from the base model, they are robust and comparable to earlier results. We expect the dynamics to be modified if more realistic information is added to the model e.g. reduced recruitment or enhanced mortality as costs associated to the antipredator behavior, or predator-dependent responses.

Table 1
A summary of the main results, indicating the effect of increasing refuge use by prey

	Mode of refuge			
	Constant proportion		Constant number	
	Predator efficiency		Predator efficiency	
	Low	High	Low	High
Local stability of equilibrium	+	+	+	Remains stable
Prey equilibrium density	+	+	+	+
Predator equilibrium density	−	−	−	−
Predator extinction probability	+	No	+	+

"+" and "−" signs indicate respectively the direct and inverse effects on the dynamic property listed at the left.

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Appendix A

Proof of Theorem 1. The system that incorporate refuge use in proportion to the prey size is given by

$$X^{\beta}: \begin{cases} \dfrac{dx}{dt} = r\left(1-\dfrac{x}{K}\right)x - y\phi(x-\beta x) \\ \dfrac{dy}{dt} = (p\phi(x-\beta x)-c)y \end{cases}$$

By considering the change of variable given by the function

$$\varphi : (\mathfrak{R}_0^+)^2 \to (\mathfrak{R}_0^+)^2 \text{ such that } \varphi(x_{(n)}, y) = \left(\frac{x_{(n)}}{1-\beta}, y\right) = (x_{(o)}, y)$$

where subindexes (n) and (o) denote the new and old variable, respectively.

We get $\det D\varphi(x_{(n)}, y) = (1/(1-\beta)) > 0$. □

Then, the vector field in the new coordinates system $Y = \varphi \circ X$ (Dumortier, 1978), has the form $Y = P(\partial/\partial x_{(n)}) + Q(\partial/\partial y)$ and the associated differential equation system is given by

$$Y^{\beta}: \begin{cases} \dfrac{dx_{(n)}}{dt} = r\left(1-\dfrac{x_{(n)}}{K(1-\beta)}\right)x_{(n)} \\ \qquad -(1-\beta)y\phi(x_{(n)}) \\ \dfrac{dy}{dt} = (p\phi(x_{(n)})-c)y \end{cases}$$

which is qualitatively equivalent to the system (1) at the first quadrant. The affirmation of Theorem 1 is corroborated by considering $K' = (1-\beta)K$.

Proof of Theorem 3. The Jacobian matrix of system (4) is

$$DZ_{\mu}(x, y) = \begin{pmatrix} 2x - 3x^2A - 2xA - y & -x \\ B(1-C)y & B(x(1-C)-AC) \end{pmatrix}$$

When $N = 1 - C - AC > 0$, the points $O = (0, 0)$ and $Q_1 = (1, 0)$ are saddle points. For the unique equilibrium point at the first quadrant we get:

$$DZ_{\mu}(x_e, y_e) = \begin{pmatrix} \dfrac{ACM}{(1-C)^2} & -\dfrac{AC}{1-C} \\ \dfrac{ABN}{1-C} & 0 \end{pmatrix}$$

with $M = 1 - C - AC - A$. As $\det DZ_{\mu}(x_e, y_e) = (A^2BCN)/(1-C)^2$, the eigenvalues depend only on $trDZ_{\mu}(x_e, y_e) = (ACM)/(1-C)^2$, and we obtain that:

(i) If $M > 0$, the point (x_e, y_e) is unstable and, according to the Poincaré-Bendixon Theorem, a limit cycle exists (Arrowsmith and Place, 1992).

(ii) If $M < 0$, the point (x_e, y_e) is locally stable.

(iii) If $M = 0$, the point (x_e, y_e) is an order one weak focus (i.e. neutrally stable cycles). □

Proof of Lemma 4.1.

(a) It is clear that, if $x = L$, we obtain $(\mathrm{d}x/\mathrm{d}\tau) = A(1-x)x > 0$, and $(\mathrm{d}y/\mathrm{d}\tau) = -ABC < 0$.

(b) For $x = 1$, we obtain $(\mathrm{d}x/\mathrm{d}\tau) = -(1-L)y < 0$, and $(\mathrm{d}y/\mathrm{d}\tau) = BHy$; i.e. independent of parameter values, any trajectory crosses the straight line $x = 1$, towards the inside of Γ, and

(c) the axis $x = 0$ is an invariant manifold of system (6). □

Proof of Lemma 4.2. The Jacobian matrix is

$$DZ_\eta^L(x, y) = \begin{pmatrix} 2x - 3x^2 - (L-A) + 2x(L-A) - y & -(x-L) \\ B(1-C)y & B(x(1-C) - L - C(-L+A)) \end{pmatrix}$$

and in (1, 0) is $DZ_\eta^L(1, 0)$

$$= \begin{pmatrix} -(1-L+A) & -(1-L) \\ 0 & BH \end{pmatrix}$$

(a) If $H > 0$, then $\det DZ_\eta^L(1, 0) = -BH(1-L+A) < 0$ and the singularity (1, 0) is a saddle point.

(b) If $H < 0$, then $\det DZ_\eta^L(1, 0) = -BH(1-L+A) > 0$, and the eigenvalues are both negative because $\mathrm{tr} DZ_\eta^L(1, 0) = -(1-L+A) + BH < 0$. The coordinate $y_e < 0$, and the point (x_e, y_e) are found in the fourth quadrant.

(c) If $H = 0$, the singularities (1, 0) and (x_e, y_e) collapse, but that singularity is nonhyperbolic. Using the Central Manifold Theorem (Guckenheimer and Holmes, 1983), it follows that the point (1, 0) is locally asymptotically stable. □

Proof of Theorem 4.3. The Jacobian matrix at the singularity (x_e, y_e) is

$$DZ_\eta^L(x_e, y_e) = \begin{pmatrix} T(A, C, L) & -\dfrac{AC}{1-C} \\ \dfrac{B(1-C)(L+AC)H}{(1-C)C} & 0 \end{pmatrix}$$

with $\det DZ_\eta^L(x_e, y_e) = (AB(1-C)(L+AC)H)/(1-C)^2$, and the sign of the eigenvalues depending only on $\mathrm{tr} D\,Z_\eta^L(x_e, y_e) = T(A, C, L) = ((3CL - L + AC^2 - AC^3 - 3C^2L + C^3L + L^2 - 3CL^2 - C^2A^2 + 3C^2L^2 - C^3A^2 - C^3L^2 - 2AC^2L + 2AC^3L)/C(1-C)^2)$

In order to analyze the sign of the trace, we consider

$$\begin{aligned} S(A, C, L) = {} & 3CL - L + AC^2 - AC^3 - 3C^2L \\ & + C^3L + L^2 - 3CL^2 - C^2A^2 + 3C^2L^2 \\ & - C^3A^2 - C^3L^2 - 2AC^2L + 2AC^3L \\ = {} & (1-C)^3L^2 - (1-C)(2AC^2 \\ & + (1-C)^2)L + AC^2(1 - C - AC - A) \end{aligned}$$

and we obtain that

(a) If $S > 0$, the singularity (x_e, y_e) of system (6) is an unstable equilibrium point, surrounded by a limit cycle.

(b) If $S < 0$, the singularity (x_e, y_e) of system (6) is a locally asymptotically stable equilibrium point. □

Proof of Theorem 5. The Jacobian matrix at (x_e, y_e) is

$$DY_\nu^L(x_e, y_e) = \begin{pmatrix} \dfrac{SL}{C(1-C)^2} & -\dfrac{CL}{1-C} \\ \dfrac{BL(1-C-L)}{(1-C)C} & 0 \end{pmatrix}$$

When $H > 0$, $\det DY_\nu^L(x_e, y_e) = (BL^2H)/(1-C)^2$, and the eigenvalues depend only on the sign of $\mathrm{tr} DY_\nu^L(x_e, y_e) = (SL)/C(1-C)^2$, which depends on the sign of $S(C, L)$

(a) If $S > 0$, then (x_e, y_e) is unstable. According to the Poincaré-Bendixon Theorem, a limit cycle exists.

(b) If $S < 0$, then (x_e, y_e) is locally asymptotically stable. □

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