

Effect of predator density dependent dispersal of prey on stability of a predator–prey system

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Dedicated to the memory of Ovide Arino

Abstract

This work presents a predator–prey Lotka–Volterra model in a two patch environment. The model is a set of four ordinary differential equations that govern the prey and predator population densities on each patch. Predators disperse with constant migration rates, while prey dispersal is predator density-dependent. When the predator density is large, the dispersal of prey is more likely to occur. We assume that prey and predator dispersal is faster than the local predator–prey interaction on each patch. Thus, we take advantage of two time scales in order to reduce the complete model to a system of two equations governing the total prey and predator densities. The stability analysis of the aggregated model shows that a unique strictly positive equilibrium exists. This equilibrium may be stable or unstable. A Hopf bifurcation may occur, leading the equilibrium to be a centre. If the two patches are similar, the predator density dependent dispersal of prey has a stabilizing effect on the predator–prey system.

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1. Introduction

Classical predator–prey models such as the Lotka–Volterra model can be used in a homogeneous environment. However, more generally, the environment is heterogeneous and this can be represented using a set of discrete patches connected by migrations. In the simplest situation, a set of two patches is used. Here, the mathematical model is composed of two parts, one describing the local predator–prey interaction and one describing the dispersal from patch to patch. There is a lot of interest in studying the effect of prey-density-dependent predator migration on the stability of a predator–prey system [1–5] and it can be assumed that prey attract predators, i.e., that predators remain on a given patch when the prey density is large and leave when it is small.

On the other hand, relatively few studies have been devoted to studying predator-density-dependent dispersal of prey. Indeed, it is realistic to assume a repulsive effect of predators on prey. The more predators there are on a patch, the larger the prey dispersal rate. An example is given by zooplankton. In aquatic environments, many zooplankton species exhibit vertical movements each day. Two main factors can explain these movements: light and food. During the day, light enhances the risk of predation by fish causing some species migrate downwards into the darkness so reducing the risk. At night, these species move upward to consume the phytoplankton produced during the day. Many authors discussed this migration behaviour. Many relates to the natural environment and references relating to the marine environment may be found in [6]. Another paper [7] describes laboratory experiments which have been developed in order to understand the underlying processes of this behaviour. In [7], the authors describe an experiment illustrating the ability of such preys to detect the risk of predation. In the case of vertical diel migration, we consider migrations to be rapid with respect to demographical processes, since the migration takes place each day (almost all the individuals move) and the demography takes place over the week or the month time scale.

In previous work, Mchich et al. [4], we considered a predator–prey model in a two patch environment. In this bioeconomical model, the prey was taken to be a fish stock and the predator a fishing fleet. We assumed that the fishing boats remained on a patch when the fish stock was large. This corresponds to the attractive effect that prey have on predators. On each patch, we assumed the classical Lotka–Volterra model with logistic growth of the prey and a type I functional response. This model, for a single isolated patch, can lead either to coexistence of prey and predator at constant densities or to predator extinction. However, the analysis of the complete model, i.e., the two patch model, has shown that the two cases of the single patch model could occur as well. We obtained a new situation with the possibility of a stable limit cycle.

Here, we study a Lotka–Volterra predator–prey model in a two patch environment. It is a system of four ordinary differential equations, governing the local predator and prey population densities. The model is composed of two parts. The first part describes the local prey and predator growth and the interactions on each patch, while the second part describes the prey and predator

dispersal between the two patches. We consider a situation where there is constant migration rates for the predators and predator-dependent migration rates for the prey population. The larger the predator density is in a patch, the more prey tend to leave it. Furthermore, we assume that there are two different time scales: one rapid, corresponding to dispersal and one slow corresponding to prey natural growth, to predator natural mortality, and to prey predator interactions. The aim of this work is to study the effects of predator-dependent migration rates of prey on the dynamics and the stability of the global system.

In Section 2, we present the predator–prey model which consists of a system of four ordinary differential equations, governing the local prey and predator population densities. The existence of two time scales enables us to build a reduced model, called the aggregated model. This reduced model is composed of two equations. It describes the dynamics of total prey and predator populations, over a slow time scale t . The aggregation of variables method (see [8–11]) is based on perturbation techniques and on the application of an adequate version of the centre Manifold Theorem [12]. In Section 3, we present the aggregated model and its equilibrium points. The stability analysis of the equilibrium points is presented in Section 4 with a discussion of the results and the ecological interpretations.

2. The prey–predator complete model

This section is devoted to the description of the predator–prey model. Let $n_1(t)$ and $n_2(t)$ be the prey population densities, at time t , located on two patches. The predators are represented by their patch population densities $p_1(t)$ and $p_2(t)$ at time t (see Fig. 1).

We assume that migrations and biotic interactions have two different characteristic time scales. Migrations are rapid and population growth rate and death rate and predation are slow. Over the rapid time scale, the total prey ($n(t) = n_1(t) + n_2(t)$) and predator ($p(t) = p_1(t) + p_2(t)$) populations are constant.

Over the slow time scale, the total prey and total predator populations (n and p) are not constant. Regarding prey equations, their dynamics in each patch, is represented by a positive term describing the natural growth and a negative term representing prey killed by predators. For the predator equations, we consider a constant natural mortality rate and assume that growth is proportional to the density of prey captured.

According to previous assumptions, the complete system, over the rapid time scale $\tau = \frac{t}{\varepsilon}$ (t is the slow time scale), reads as follows:

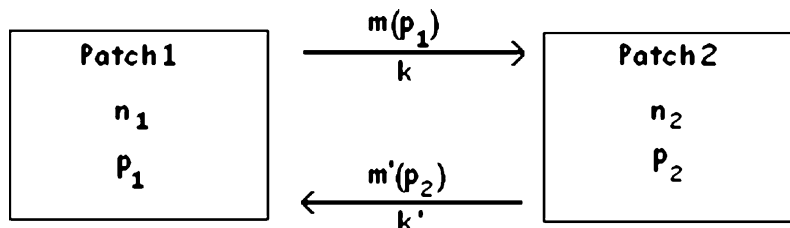


Fig. 1. Illustration of the migration of prey and predators on two patches.

$$\begin{cases} \frac{dn_1}{d\tau} = (m'(p_2)n_2 - m(p_1)n_1) + \varepsilon[r_1n_1 - a_1n_1p_1], \\ \frac{dn_2}{d\tau} = (m(p_1)n_1 - m'(p_2)n_2) + \varepsilon[r_2n_2 - a_2n_2p_2], \\ \frac{dp_1}{d\tau} = (k'p_2 - kp_1) + \varepsilon[-m_1p_1 + b_1n_1p_1], \\ \frac{dp_2}{d\tau} = (kp_1 - k'p_2) + \varepsilon[-m_2p_2 + b_2n_2p_2], \end{cases} \quad (2.1)$$

where r_i ($i = 1, 2$) represent the intrinsic growth rate of the prey population in patch i . Patches have distinct characteristics, so we assume that parameters r_1 and r_2 can be different. We have considered the simplest type I functional response on each patch. a_i and b_i are predation parameters on patch i . The term m_i is the natural mortality rate of the predator in patch i . Constant parameters k and k' represent the predator migration rates from patch 1 to patch 2 and inversely. The prey migration rates are predator density dependent as follows:

$$m(p_1) = \alpha p_1 + \alpha_0 \quad \text{and} \quad m'(p_2) = \beta p_2 + \alpha_0.$$

The more predators found on a patch, the more the prey tend to leave this patch. In other words, predators tend to increase the migration rate of the prey in each patch. Note that α_0 , α and β are positive parameters. ε is a small dimensionless parameter meaning that biotic processes are assumed to be slow.

3. The aggregated model

This section is devoted to the construction of the aggregated model. The first step is to neglect the slow part of the equations and to study the rapid dispersal model. Let us first calculate the rapid equilibrium. For this, we first define

$$n(t) = n_1(t) + n_2(t) \quad \text{and} \quad p(t) = p_1(t) + p_2(t)$$

to be the total prey (respectively, predator) density and we set $\varepsilon = 0$ in the system (2.1). We calculate the equilibria of the obtained system. After some simple calculations, we obtain the following equilibria for the rapid part of the system:

$$\begin{cases} p_1^* = \mu_1 p, & p_2^* = \mu_2 p, \\ n_1^* = \eta_1(p)n, & n_2^* = \eta_2(p)n, \end{cases} \quad (3.1)$$

where μ_i represents the rapid equilibrium proportion of the predator population on patch i , while $\eta_i(p)$ gives the same interpretation for the prey population on zone i . All these proportions are given by:

$$\begin{cases} \mu_1 = \frac{k'}{k+k'}, & \mu_2 = \frac{k}{k+k'}, \\ \eta_1(p) = \frac{\alpha_0 + \beta\mu_2 p}{2\alpha_0 + \delta p}, & \eta_2(p) = \frac{\alpha_0 + \alpha\mu_1 p}{2\alpha_0 + \delta p}, \end{cases} \quad (3.2)$$

where

$$\delta := \alpha\mu_1 + \beta\mu_2.$$

Now, coming back to the complete initial system (2.1), we substitute the rapid equilibria (3.1) and add the two equations of the local prey and predator population densities (see the aggregation methods in [8–11]). We obtain the following system, when using the slow time scale t :

$$\begin{cases} \dot{n}(t) = \frac{1}{\delta p + 2\alpha_0}(rn + anp - \bar{b}np^2), \\ \dot{p}(t) = -Mp + \frac{1}{\delta p + 2\alpha_0}(bnp + cnp^2), \end{cases} \quad (3.3)$$

where

$$\begin{cases} r = \alpha_0(r_1 + r_2), \\ a = r_1\beta\mu_2 + r_2\alpha\mu_1 - \alpha_0(a_1\mu_1 + a_2\mu_2), \\ \bar{b} = \mu_1\mu_2(a_1\beta + a_2\alpha), \\ M = m_1\mu_1 + m_2\mu_2, \\ b = \alpha_0(b_1\mu_1 + b_2\mu_2), \\ c = \mu_1\mu_2(b_1\beta + b_2\alpha). \end{cases}$$

Since, for each value of total prey and predator densities, the rapid equilibrium (obtained with $\varepsilon = 0$) is hyperbolically stable, the set of rapid equilibria obtained when ε is null, leads to an attracting two-dimensional invariant set for small positive values of ε [11]. The reduced model (3.3) is an ε -approximation of the restriction of the complete model to this invariant two-dimensional set. We use the reduced model (3.3) to study the dynamics of the complete system (2.1). More precisely, the complete model dynamics belongs to a four-dimensional space where a two-dimensional invariant set attracts the trajectories. The dynamics restricted to this two-dimensional set can be approximated by a Taylor expansion with respect to the small parameter ε . The first order expansion leads to the aggregated model. Thus, the real dynamics is an ε -perturbation of that described by the aggregated model. If the aggregated model dynamics is structurally stable and ε is small enough, then the dynamics of the aggregated model gives a good idea of the behaviour of the complete model trajectories. Now, we are going to proceed to the analysis of the aggregated model (3.3) (for details, see the [Appendix](#)).

The n -nullclines are given by

$$n = 0 \quad \text{and} \quad p = \frac{a + \sqrt{a^2 + 4rb}}{2\bar{b}}.$$

The p -nullclines are given by

$$p = 0 \quad \text{and} \quad p = \frac{-bn + 2\alpha_0 M}{cn - M\delta}.$$

So, we have two equilibrium points:

- $(0, 0)$ which is always a saddle point;
- (n^*, p^*) , where

$$n^* = \frac{M(\delta p^* + 2\alpha_0)}{ep^* + b} \quad \text{and} \quad p^* = \frac{a + \sqrt{a^2 + 4rb}}{2\bar{b}}. \quad (3.4)$$

The Jacobian matrix of the equilibrium point (n^*, p^*) has a trace B given by

$$B := \frac{p^*M(2\alpha_0c - \delta b)}{(b + cp^*)(\delta p^* + 2\alpha_0)}. \quad (3.5)$$

Then, for the stability of the equilibrium point (n^*, p^*) , two situations occur:

1. *Case 1:* If $B < 0$, (n^*, p^*) is a stable equilibrium (focus or node).
2. *Case 2:* If $B > 0$, then (n^*, p^*) is an unstable equilibrium.

Remark 1. The term B (given by (3.5)) can be equal to zero, and in this case, the linearization of the aggregated model is not sufficient to conclude any information about the dynamics of the non-linear aggregated model.

When B crosses the zero value, a Hopf bifurcation occurs. Now, we shall show that this bifurcation is degenerate and that, at the bifurcation $B = 0$, the dynamics is a centre on the whole positive quadrant. We first prove this result for the system (3.3) but it is still valid for an ε -perturbation of system (3.3) as we will see later. With respect to the complete system (2.1), this result proves that the trajectories of the complete model do not tend towards a limit cycle since there is no limit cycle. This result is not obvious a priori since, generically, a Hopf bifurcation is associated to the apparition or the disappearance of a limit cycle. This is why we deduce that, in our case, the Hopf bifurcation is degenerate.

In order to show that there is a centre for the reduced system, we are going to demonstrate that, for any $B \neq 0$, the aggregated model cannot have closed orbits by use of the negative *Dulac's criterion* (see [13,14]). We consider a simply connected domain D defined by the positive quadrant which is positively invariant as the n and p axis are nullclines.

If we set

$$F(n, p) := \frac{\dot{n}}{n \cdot p} \quad \text{and} \quad G(n, p) := \frac{\dot{p}}{n \cdot p},$$

then, we get:

$$F(n, p) := \frac{1}{\delta p + 2\alpha_0} \left(\frac{r}{p} + a - \bar{b}p \right),$$

$$G(n, p) := -\frac{M}{n} + \frac{1}{\delta p + 2\alpha_0} (b + cp),$$

so, we have

$$\frac{\partial F}{\partial n} = 0 \quad \text{and} \quad \frac{\partial G}{\partial p} = \frac{2\alpha_0 c - \delta b}{(\delta p + 2\alpha_0)^2}.$$

As the expression $\frac{\partial F}{\partial n} + \frac{\partial G}{\partial p}$ does not change sign in the connected domain D , and by using the Dulac's criterion and the Poincaré–Bendixon theorem, we can conclude that when $B \neq 0$ (B is given by (3.5)) then there is not a closed orbit. More precisely, when $B > 0$, the equilibrium (n^*, p^*) becomes unstable while when $B < 0$, this equilibrium is globally asymptotically stable.

In order to show the centre, let us consider a half straight line Σ containing the equilibrium point and contained in the positive quadrant. On Σ , we can define a map P_0 by considering for each point $m_0 \in \mathbb{R}$, the point $m \in \mathbb{R}$ obtained by the first intersection between Σ and the positive orbit starting from m_0 . This application is called the Poincaré map. It allows us to define the displacement function

$$\Delta_0(m) = P_0(m) - m,$$

which is useful in detecting the closed orbits.

Indeed, if a closed orbit exists, let m_0 be the intersection point between this closed orbit and Σ , then $\Delta_0(m_0) = 0$. If $\Delta_0(m) > 0$ then the trajectory starting from m moves away from the equilibrium, while if $\Delta_0(m) < 0$, then the trajectory starting from m is moving towards equilibrium.

The Dulac criteria mentioned above enables us to conclude that $\Delta_0 < 0$ for all m if, and only if, $B < 0$ and $\Delta_0 > 0$ for all m if, and only if, $B > 0$. It follows that when $B = 0$, $\Delta_0 \equiv 0$ and the system (3.3) exhibits a centre: all the orbits are closed.

We have shown that the aggregated model always has a positive equilibrium. The parameter B is a bifurcation parameter. When $B < 0$, the previous equilibrium is globally asymptotically stable while when $B > 0$, the equilibrium is globally asymptotically unstable. When the sign of B changes, there is a degenerate Hopf bifurcation and when $B = 0$ the equilibrium is a centre and all the trajectories are closed. Now, it is necessary to prove that the previous description is still valid for the complete model dynamics. Indeed, as we explained earlier, the complete dynamics is described by a system which can be written as an ε -perturbation of the aggregated model. Thus, at this step, we can only conclude that if $B < 0$ and ε is small enough, then the complete model has a globally asymptotically stable equilibrium and that if $B > 0$ and ε is small enough, then the complete model has a globally asymptotically unstable equilibrium. Now, let us fix ε to a small value and describe the dynamics for B which is close to the bifurcation value 0. We shall show that the centre still exists, that is for a ε -perturbation of (3.3), for a B value close to 0.

We again base our arguments on the Dulac negative criteria. The restriction of the complete four-dimensional model to the two-dimensional subset can be written as follows:

$$\begin{cases} \dot{n}(t) = np(F(n, p) + \varepsilon F_1(n, p, \varepsilon)), \\ \dot{p}(t) = np(G(n, p) + \varepsilon G_1(n, p, \varepsilon)). \end{cases} \quad (3.6)$$

As previously, by dividing the previous vector field by np in the positive quadrant, if the sign of the following expression is constant then there is no closed orbit in the positive quadrant

$$E = \frac{\partial}{\partial n}(F(n, p) + \varepsilon F_1(n, p, \varepsilon)) + \frac{\partial}{\partial p}(G(n, p) + \varepsilon G_1(n, p, \varepsilon)).$$

If the previous expression is positive for every (n, p) in the positive quadrant, then the positive equilibrium of (3.6) is globally asymptotically unstable while if the previous expression is negative for each (n, p) in the positive quadrant, then the positive equilibrium of (3.6) is globally asymptotically stable. Now, we can write E as follows:

$$E = \frac{B(b + cp)}{pM(\delta p + 2\alpha_0)} + \varepsilon \phi(n, p, \varepsilon) = H(\varepsilon, B).$$

Obviously, we have

$$H(0, 0) = 0$$

and

$$\frac{\partial H}{\partial B}(\varepsilon, B) = \frac{(b + cp)}{pM(\delta p + 2\alpha_0)} + \varepsilon \frac{\partial \phi}{\partial B}(n, p, \varepsilon),$$

which leads to

$$\frac{\partial H}{\partial B}(0, 0) = \frac{(b + cp)}{pM(\delta p + 2\alpha_0)} > 0.$$

Using the implicit function theorem, there is a function h in the vicinity of 0 such that

$$H(\varepsilon, B) = 0 \iff B = h(\varepsilon). \quad (3.7)$$

In other words, for $B = h(\varepsilon)$, which is close to 0 when ε is close to 0, $H(\varepsilon, h(\varepsilon)) \equiv 0$. Let $P_\varepsilon(m)$ be the Poincaré map associated to the perturbation (3.6) of the aggregated model. We define

$$\Delta_\varepsilon(m) = P_\varepsilon(m) - m.$$

Thus, for $B = h(\varepsilon)$, $\Delta_\varepsilon \equiv 0$ on the positive quadrant.

Indeed, let us denote the positive quadrant by Ω . When $B > h(\varepsilon)$ then $H(\varepsilon, B) > 0$ and thus $\Delta_\varepsilon(m) > 0$ for all $m \in \Omega$. Similarly, when $B < h(\varepsilon)$, $\Delta_\varepsilon(m) < 0$ for all $m \in \Omega$. Finally, $\Delta_\varepsilon(m) = 0$ for all $m \in \Omega$ when $B = h(\varepsilon)$.

As a consequence, there is a centre for the system (3.6), the Hopf bifurcation occurring for B crossing $h(\varepsilon)$ is degenerate.

4. Discussion and conclusion

The analysis of the aggregated model (3.3) presents three main situations:

- The non-trivial equilibrium (n^*, p^*) given by (3.4) is globally asymptotically stable. In this case, prey and predator coexist with constant densities on each patch.
- The non-trivial equilibrium (n^*, p^*) is unstable. The predator–prey community is not persistent. Indeed, numerical simulations (Fig. 2) show that, after some time, the trajectories pass very close to the n or p axis which would lead, in a real situation, to predator extinction and unbounded prey growth or to prey extinction followed by predator extinction.
- The non-trivial equilibrium is a centre. In this case, Fig. 3 shows that there are closed trajectories. Predator and prey densities cycle with an amplitude depending on the initial condition.

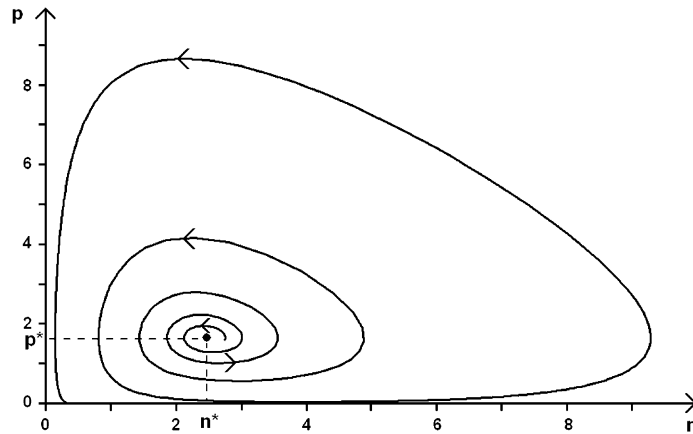


Fig. 2. Phase portrait in the case of an unstable equilibrium: ($n^* = 2.465$, $p^* = 1.651$). We see clearly that the trajectory tends to the extinction of prey or predators. Parameters have been chosen as: $\delta = 2$, $\alpha_0 = 1$, $r = 0.5$, $a = 1$, $\bar{b} = 2$, $M = 2$, $b = 1$ and $c = 2$.

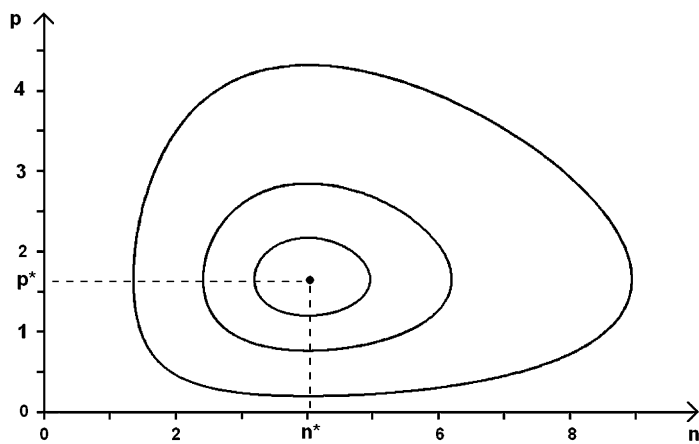


Fig. 3. Phase portrait in the case where $b\bar{b} = 2\alpha_0 c$. Here, we see clearly that the equilibrium point presents a centre. Parameters have been chosen as: $\delta = 2$, $\alpha_0 = 1$, $r = 0.5$, $a = 3$, $\bar{b} = 2$, $M = 2$, $b = 1$ and $c = 1$.

It is useful to compare the qualitative dynamics of the local model on each isolated patch to the one of the aggregated model. The local model is the classical Lotka–Volterra model with a type I functional response. Therefore, on each isolated patch, if dispersal were impossible, we expect periodic solutions corresponding to a centre. When the patches are connected by migrations, the dynamics of the complete two patch model (2.1) is described by the aggregated model (3.3) for which we can have predator–prey coexistence, non-persistence or for a given value of parameters cyclic population densities.

As a consequence, the qualitative dynamics of the single patch and of the two patch model are different. This difference comes from the assumption we have made that the predator repulsion

effects prey dispersal. As a consequence, we can consider that this repulsive effect can promote stability in the case of a stable equilibrium.

Let us try to interpret the term B which is the trace of the Jacobian matrix, in the neighbourhood of the equilibrium point (n^*, p^*) given by (3.4). The trace can be rewritten as follows:

$$B = \frac{-\alpha_0 M}{D} \Delta_{\text{mig}} (b_1 \mu_1 - b_2 \mu_2),$$

where Δ_{mig} is given by

$$\Delta_{\text{mig}} := m(p_1) - m'(p_2)$$

or

$$\Delta_{\text{mig}} = (\alpha \mu_1 - \beta \mu_2) p^*,$$

and D is given by

$$D := (b + c p^*)(\delta p^* + 2\alpha_0).$$

First, let us study the simplest scenario when the two patches are assumed to be similar, except for predator migration rates k and k' , i.e., we assume that $\alpha = \beta$ and $b_1 = b_2$, but $\mu_1 \neq \mu_2$. Then, the trace of the Jacobian matrix becomes

$$B = -\frac{\alpha \alpha_0 b_1 M}{D} (\mu_1 - \mu_2)^2 p^* < 0$$

and, in this case, the equilibrium point (n^*, p^*) is globally asymptotically stable.

If $\mu_1 = \mu_2$, then the equilibrium point (n^*, p^*) is neutrally stable, and there are periodic solutions. As a consequence, in the scenario where the two patches are similar, the non-trivial equilibrium is stable.

Now, let us suppose that $\mu_1 > \mu_2$ (which means that, over a short time scale, there are more predators on patch 1 than on patch 2) and that b_1 is close to b_2 . To have a stable equilibrium at (n^*, p^*) , we must have $\Delta_{\text{mig}} > 0$. Thus the greater α is to β , the greater the stability of the system.

On the other hand, we have studied the system (2.1) in the situation where

$$m(p_1) = \alpha_0 + \alpha \cdot p_1^h \quad \text{and} \quad m(p_2) = \alpha_0 + \beta \cdot p_2^h,$$

where h is an integer greater than 1. The results, which are not shown here, gave the same qualitative stability. We also obtained three situations for this model: a stable equilibrium, an unstable equilibrium or a centre.

Another situation worth considering is that of a spatial network of several patches connected by migrations. One can also investigate the scenario where the prey natural growth is of logistic type.

On the other hand, it is realistic to assume that, at the same time, there is a repulsive effect of predators on prey and that prey attract predators. So, another interesting case to study is a repulsive-attractive model; i.e., one can assume that when the predator density is large on a patch, the prey dispersal rate is large too, and at the same time, one will assume that predators will remain on a given patch when the prey density is large and leave it when it is small, and so on.

Acknowledgments

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Appendix

In this section, we provide details with regard to the mathematical analysis of system (3.3).

The n -nullclines of system (3.3) are given by

$$n = 0 \quad \text{and} \quad -\bar{b}p^2 + ap + r = 0,$$

the second n -nullcline has one positive root, given by

$$p = \frac{a + \sqrt{a^2 + 4r\bar{b}}}{2\bar{b}}.$$

The p -nullclines are given by:

$$p = 0 \quad \text{and} \quad -M\delta p - 2\alpha_0 M + nb + cpn = 0,$$

the second p -nullcline can be written as

$$p = \frac{-bn + 2\alpha_0 M}{cn - M\delta} \quad \text{or} \quad n = \frac{M(\delta p + 2\alpha_0)}{cp + b}.$$

According to the parameter values, there are two situations:

1. *Case 1:* If $2\alpha_0 c - b\delta < 0$, we can produce Fig. 4.
2. *Case 2:* If $2\alpha_0 c - b\delta > 0$, we can produce Fig. 5.

In either case, we have two equilibrium points: $(0, 0)$ and (n^*, p^*) , given by (3.4).

The Jacobian matrix of the system (3.3) reads as follows:

$$J(n, p) = \begin{bmatrix} \frac{r + ap - \bar{b}p^2}{\delta p + 2\alpha_0} & n \frac{(a - 2\bar{b}p)(\delta p + 2\alpha_0) - \delta(r + ap - \bar{b}p^2)}{(\delta p + 2\alpha_0)^2} \\ \frac{bp + cp^2}{\delta p + 2\alpha_0} & -M + \frac{n(b + cp)}{\delta p + 2\alpha_0} + np \frac{c(\delta p + 2\alpha_0) - \delta(b + cp)}{(\delta p + 2\alpha_0)^2} \end{bmatrix}.$$

- For the equilibrium point $(0, 0)$, we have

$$J(0, 0) = \begin{bmatrix} \frac{r}{2\alpha_0} & 0 \\ 0 & -M \end{bmatrix}.$$

This matrix has two real eigenvalues with opposite signs: $\frac{r}{2\alpha_0}$ and $-M$, so $(0, 0)$ is always a saddle point.

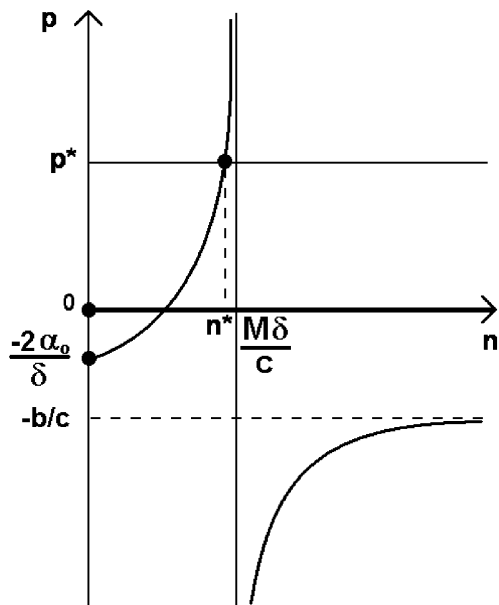


Fig. 4. Illustration of isoclines in the case where $b\delta - 2\alpha_0 c > 0$. So in this case, (n^*, p^*) is a stable equilibrium (node or focus).

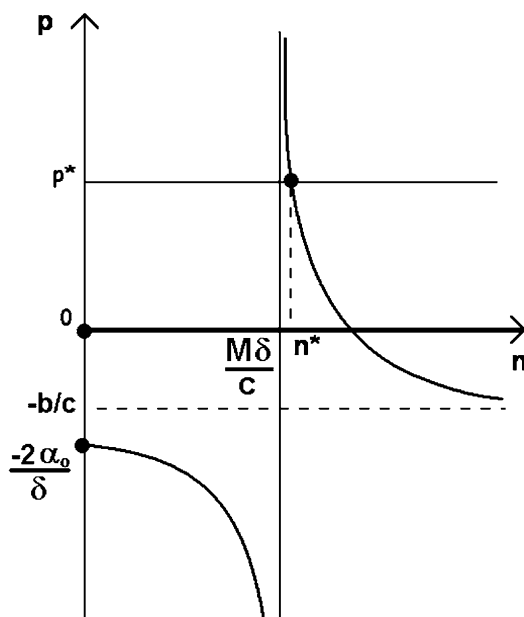


Fig. 5. Illustration of isoclines in the case where $b\delta - 2\alpha_0 c < 0$. So in this case, (n^*, p^*) is an unstable equilibrium (node or focus).

- For the equilibrium point (n^*, p^*) (given by (3.4)), we have

$$J(n^*, p^*) = \frac{1}{(b + cp^*)(\delta p^* + 2\alpha_0)} \begin{bmatrix} 0 & M(2\alpha_0 a - \bar{b}\delta p^{*2} - 4\bar{b}\alpha_0 p^* - \delta r) \\ p^*(b + cp^*)^2 & p^*M(2\alpha_0 c - \delta b) \end{bmatrix}.$$

This matrix has a positive determinant C :

$$C := \frac{p^*M}{(\delta p^* + 2\alpha_0)^2} (\bar{b}\delta p^{*2} + 4\bar{b}\alpha_0 p^* + \delta r - 2\alpha_0 a), \quad (\bar{b}\delta p^{*2} + 4\bar{b}\alpha_0 p^* + \delta r - 2\alpha_0 a) > 0,$$

$$\text{because: } 4\bar{b}\alpha_0 p^* - 2\alpha_0 a = 2\alpha_0 \sqrt{a^2 + 2r\bar{b}} > 0.$$

Let B be the trace of the Jacobian matrix (given by (3.5)), and $\Delta := B^2 - 4C$. Thus, we have two eigenvalues for the Jacobian matrix $J(n^*, p^*)$ given by:

$$\lambda_1 = \frac{B - \sqrt{\Delta}}{2} \quad \text{and} \quad \lambda_2 = \frac{B + \sqrt{\Delta}}{2} \quad \text{if } \Delta > 0$$

or

$$\lambda_1 = \frac{B - i\sqrt{-\Delta}}{2} \quad \text{and} \quad \lambda_2 = \frac{B + i\sqrt{-\Delta}}{2} \quad \text{if } \Delta < 0.$$

Then, for the stability of the equilibrium point (n^*, p^*) (given by (3.4)), two situations arise:

1. *Case 1:* If $B < 0$, we have either two negative real eigenvalues (when $\Delta > 0$) or two complex eigenvalues with negative real parts (when $\Delta < 0$): and in both cases, (n^*, p^*) is a stable equilibrium (focus or node).
2. *Case 2:* If $B > 0$, we have either two positive real eigenvalues (when $\Delta > 0$) or two complex eigenvalues with positive real parts (when $\Delta < 0$): and in both cases (n^*, p^*) is an unstable equilibrium.

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