

EFFECTS OF DENSITY DEPENDENT MIGRATIONS ON THE DYNAMICS OF A PREDATOR PREY MODEL

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ABSTRACT

We study the effects of density dependent migrations on the stability of a predator-prey model in a patchy environment which is composed with two sites connected by migration. The two patches are different. On the first patch, preys can find resource but can be captured by predators. The second patch is a refuge for the prey and thus predators do not have access to this patch. We assume a repulsive effect of predator on prey on the resource patch. Therefore, when the predator density is large on that patch, preys are more likely to leave it to return to the refuge. We consider two models. In the first model, preys leave the refuge to go to the resource patch at constant migration rates. In the second model, preys are assumed to be in competition for the resource and leave the refuge to the resource patch according to the prey density. We assume two different time scales, a fast time scale for migration and a slow time scale for population growth, mortality and predation. We take advantage of the two time scales to apply aggregation of variables methods and to obtain a reduced model governing the total prey and predator densities. In the case of the first model, we show that the repulsive effect of predator on prey has a stabilizing effect on the predator-prey community. In the case of the second model, we show that there exists a window for the prey proportion on the resource patch to ensure stability.

Key Words: predator prey model, refuge, resource, time scales, aggregated model, stability, Dulac's criterion.

1. INTRODUCTION

There was a lot of interest for the study of the effect of a prey refuge on the stability of predator-prey communities (one can see Chiorino et al., 1999; González-Olivares and Ramos-Jilibert, 2003; Hausrath, 1994; Kar, 2004; Křivan, 1998; Srinivasu and Gayatri, 2005; Yakubu, 1997). In the case of a refuge for preys, the environment is heterogeneous and is usually represented by a set of discrete patches connected by migrations, see Chiorino et al. (1999), Ives (1992), Mchich et al. (2002, 2004) and Reeve (1988). The simplest situation corresponds to a set of two patches. The mathematical model is thus composed of two parts, a part which describes local predator-prey interactions on each patch and a part which describes the migration from patch to patch, for example from

the refuge to another patch where preys can go. It is also realistic to assume that prey as well as predator migrations are density-dependent. In some cases, it is also realistic to assume that prey and predator migration occurs at a fast time scale in comparison to population growth, mortality and predation. In these cases (see Auger et al., 2000; Auger and Poggiale, 1996, 1998; Mchich et al., 2002), a reduced model governing the time evolution of total prey and predator densities (obtained by summation of prey and predator densities over all patches) can be derived. This aggregated model is useful to study the effects of density-dependent migrations on the stability of the predator-prey system in the long term.

In this work, we deal with a predator-prey model in a heterogeneous environment composed by two spatial patches, on which a population of preys $N(t)$, subdivided into two subpopulations: $N_1(t)$ on patch 1 and $N_2(t)$ on patch 2 can move. We assume that there is a population of predators $P(t)$ present only on patch 1. So the patch 2 can be considered as a refuge site for the prey. On another hand, we also assume that, on patch 2, there is only mortality for preys (and no natural growth), so preys must leave patch 2 to patch 1, in order to have access to a resource. It is also assumed that when there are many predators on patch 1, in order to escape predation, preys leave this patch to return to their refuge. We present two different scenarios of the predator prey model in this patchy environment with two sites connected by preys migration flows.

We also assume that migration is faster than growth, mortality and predation. So, models contain two time scales: a fast one associated to the migration and a slow one corresponding to the growth, the mortality and the predation. Then, we take advantage of the two time scales to reduce the complete models by use of the so known aggregation methods (one can see the review article on aggregation techniques by Auger and Bravo de la Parra (2000)). The method is based on perturbation technics and on the application of an adequate version (one can see Auger and Poggiale, 1996; Auger and Roussarie, 1994; Michalski et al., 1997; Poggiale, 1994) of the Center Manifold Theorem (see Fenichel, 1971). The aggregation of the complete model consists in supposing that the fast dynamics has attained a stable equilibrium and in substituting this fast equilibrium into the equations of the complete model. Therefore, we obtain a reduced model which describes the dynamics of the global population of preys and predators, and has the advantage that it is possible to perform its complete qualitative analysis.

In Section 2, we present two mathematical models, which consist on a prey population migrating between two patches, a resource patch and a refuge. In both models, we assume a predator-density dependent migration rate for the prey, from patch 1 to patch 2. In model I, we also consider constant migration rate in the other sense while in model II, we consider a repulsive effect between preys on patch 2. By applying the aggregation methods, in both cases, we derive a reduced model governing the total prey and predator densities. We perform the stability analysis of the aggregated models which allows us to compare the effects of different density dependent migration functions on the stability of the predator prey system. Section 3 is devoted to discussion and ecological interpretations.

2. PRESENTATION OF THE PREDATOR PREY MODELS

We consider a prey population with total density $N(t)$ at time t in a patchy environment with two patches. Patch 1 is a resource patch where preys must come to feed but face

predation. Patch 2 is a prey refuge and predators cannot have an access to this patch. Let $N_1(t)$ be the prey density on the resource patch and $N_2(t)$ the prey density in the refuge. Predator is assumed to always remain on the resource patch. We also assume that there is no resource for the prey in the refuge and therefore preys must migrate from the refuge to the resource patch, to look for resources (see Figures 1 and 2). We are going to study the effects of density dependent migrations of preys from the refuge to the resource patch on the stability of the predator prey community.

2.1. Predator Prey Model I

2.1.1. The complete model I

In model I, preys leave the resource patch according to the predator density on that patch. When there are many predators, preys are more likely to return to the refuge. Assuming that preys must find resource regularly, the migration flow of preys from refuge to resource patch is constant. We also assume two time scales, a fast one, τ , which corresponds to prey migration, and a slow time scale, t , which corresponds to the growth of the prey population, the prey mortality in its refuge, the predator mortality and the predation. We use time scale separation methods, also refereed as “aggregation of variables methods”, to obtain a reduced model governing the total prey and predator population densities. For aggregation methods in population dynamics, we refer to Auger and Bravo de la Parra (2000), Chiorino et al. (1999) and Mchich et al. (2002, 2004).

According to previous assumptions, the complete model I, at the fast time scale $\tau = \epsilon t$, is a system of three nonlinear ordinary differential equations and reads as follows:

$$\begin{cases} \frac{dN_1}{d\tau} = (\alpha N_2 - \beta P N_1) + \epsilon[rN_1 - aN_1 P] \\ \frac{dN_2}{d\tau} = (\beta N_1 P - \alpha N_2) + \epsilon[-mN_2] \end{cases} \frac{dP}{d\tau} = \epsilon[-\mu P + bN_1 P] \tag{2.1}$$

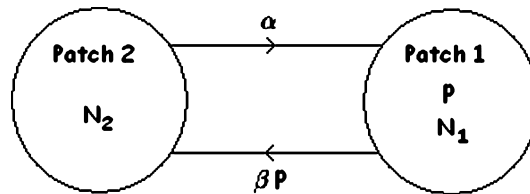


Figure 1. Illustration of the preys and predators migration on two patches for model I.

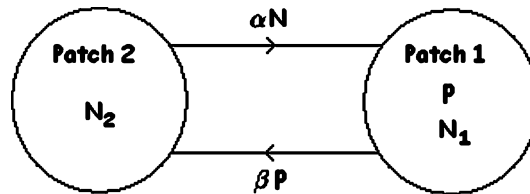


Figure 2. Illustration of the preys and predators migration on two patches for model II.

where α ($\alpha > 0$) is the prey migration rate from patch 2 to patch 1 and βP ($\beta > 0$) is the prey migration rate in the opposite sense, depending on P . The term r represents the intrinsic growth rate of the prey population on patch 1. The parameter m represents the prey mortality rate on patch 2, while μ is the predator mortality rate. The term a is the predator-prey predation rate per unit of time, while b is the conversion rate of prey biomass into predator biomass. a , b , m and μ are all positive constants. ε is a small dimensionless parameter.

2.1.2. The aggregated model I

To obtain a reduced model, the aggregated model, we first set $\varepsilon = 0$ in the complete model (2.1). In this way, we neglect the slow terms of the complete model and we consider only the fast dynamics. In our case, the fast process is prey migration described by the following two equations:

$$\begin{cases} \frac{dN_1}{d\tau} = (\alpha N_2 - \beta N_1 P) \\ \frac{dN_2}{d\tau} = (\beta N_1 P - \alpha N_2) \end{cases} \quad (2.2)$$

The next step is to look for the existence of a stable fast equilibrium. Migration is conservative because preys leaving the refuge go to the resource patch. Therefore, the total prey density N remains constant at the fast time scale. Then, N_2 can be replaced by $N - N_1$, and we obtain the next expressions of the fast equilibrium:

$$\begin{cases} N_1^* = \frac{\alpha N}{\alpha + \beta P} \\ N_2^* = \frac{\beta N P}{\alpha + \beta P} \end{cases} \quad (2.3)$$

The following step is to substitute the fast equilibrium (2.3) into the equations of the complete system (2.1), and to add the two first equations of the system (2.1), to obtain the aggregated system at the slow time scale:

$$\begin{cases} \frac{dN}{dt} = \frac{N}{(\alpha + \beta P)} [r\alpha - (a\alpha + m\beta)P] \\ \frac{dP}{dt} = \frac{P}{(\alpha + \beta P)} [-\mu\alpha + b\alpha N - \mu\beta P] \end{cases} \quad (2.4)$$

This aggregated model is obtained by assuming that the fast dynamics tends very fast to the fast stable equilibrium. This is an approximation which is valid when ε is small enough and when the aggregated model is structurally stable. We are now going to use the aggregated model to study the stability property of the predator prey system in the long term.

The aggregated model has two positive equilibrium points: $(0, 0)$ and (N^*, P^*) , where:

$$\left\{ N^* = \frac{1}{b} \left(\frac{r\mu\beta}{a\alpha + m\beta} + \mu \right) P^* = \frac{r\alpha}{a\alpha + m\beta} \right. \quad (2.5)$$

It is easy to check that $(0, 0)$ is a saddle point, while (N^*, P^*) is a stable (node or focus) equilibrium (see appendix). In any case, whatever are the values of the parameters of the

model, the unique positive equilibrium of the aggregated model is locally asymptotically stable.

2.2. Predator Prey Model II

2.2.1. The complete predator prey model II

In the case of model II, we assume that prey density has also an effect on prey migration. When the total prey density is large and for a limited resource, the average available amount of resource per prey is decreasing. Therefore, we assume that preys must come more frequently to the resource patch to feed. In the complete model II, we thus consider that the prey migration rate from the refuge to the resource patch is proportional to the total prey density.

According to these assumptions, the complete model II reads as follows:

$$\begin{cases} \frac{dN_1}{d\tau} = (\alpha NN_2 - \beta PN_1) + \varepsilon[rN_1 - aN_1P] \\ \frac{dN_2}{d\tau} = (\beta PN_1 - \alpha NN_2) + \varepsilon[-mN_2] \\ \frac{dP}{d\tau} = \varepsilon[-\mu P + bN_1P] \end{cases} \quad (2.6)$$

2.2.2. The aggregated model II

In this case, there exists a unique fast and stable equilibrium which is given by:

$$\left\{ N_1^* = \frac{\alpha N^2}{\alpha N + \beta P} N_2^* = \frac{\beta NP}{\alpha N + \beta P} \right.$$

Substituting the fast equilibrium into the complete model II (2.6), and adding the prey equations, we obtain the aggregated model II:

$$\begin{cases} \frac{dN}{dt} = \frac{N}{(\alpha N + \beta P)} [r\alpha N - (\alpha\alpha N + m\beta)P] \\ \frac{dP}{dt} = \frac{P}{(\alpha N + \beta P)} [-\mu\alpha N + b\alpha N^2 - \mu\beta P] \end{cases} \quad (2.7)$$

This aggregated model has a single equilibrium point (see appendix for details) in the positive quadrant (N^*, P^*) , where :

$$\begin{cases} N^* = \frac{(\alpha\alpha\mu - bm\beta) + \sqrt{\bar{\Delta}}}{2ab\alpha} \\ P^* = \frac{r\alpha N^*}{\alpha\alpha N^* + m\beta} \end{cases} \quad (2.8)$$

with

$$\bar{\Delta} = 4ab\alpha\beta\mu(m+r) + (bm\beta - \alpha\alpha\mu)^2.$$

The stability of the equilibrium point (N^*, P^*) depends on the sign of the constant B :

$$B := -\mu + \frac{\mu^2}{bN^{*2}} + \frac{m\beta P^*}{\alpha N^* + \beta P^*} \quad (2.9)$$

Three cases can occur(see appendix for details):

- When $B > 0$, then (N^*, P^*) is a stable equilibrium (node or focus).
- When $B < 0$, then (N^*, P^*) is a unstable equilibrium.
- When $B = 0$, then (N^*, P^*) is a center. In this case, by use of the negative *Dulac's criterion* (see Arrowsmith and Place, 1992; Edelstein-Keshet, 1998), we can show that there are no closed orbits.

3. DISCUSSION

In the case of aggregated model I (2.4), there exist two equilibrium points: $(0, 0)$ which is a saddle point, and (N^*, P^*) which is always a stable equilibrium. As a consequence, in this case, the repulsive effect of predator on preys has a stabilizing effect on the predator prey system. Indeed, on the refuge, preys die and without migration to the resource patch, the prey population would decay and go extinct. On the resource patch, preys are captured by predators. If preys would remain all the time on this patch, prey and predator densities would vary periodically according to the Lotka-Volterra model. Large variations of prey and predator densities are expected to occur for some initial conditions leading to the possibility of population extinction when the densities are close to zero. However, when the two patches are coupled by migration of preys, whatever are the values of all parameters, the predator and the prey coexist in the long term. After some transient dynamics, and for any initial condition in the positive quadrant, the prey and predator densities tend to constant densities corresponding to the stable equilibrium of the aggregated model I.

In the case of aggregated model II (2.7), there exists a positive and unique equilibrium which can be either stable, unstable or a center. Therefore, the need for preys to go more frequently on the resource patch when the total prey density increases has a destabilizing effect on the predator prey system with respect to the previous case.

Let us try now to interpret the condition $B > 0$ (B is given by (2.9)), which leads to a stable equilibrium. We have:

$$B := -\mu + \frac{\mu^2}{bN^{*2}} + \frac{m\beta P^*}{\alpha N^* + \beta P^*}.$$

At the fast equilibrium, we have $mv_2 = m \frac{N_2^*}{N^*} = \frac{m\beta P^*}{\alpha N^* + \beta P^*}$, and at the equilibrium we also have $\mu = bN_1^*$. So, B can be rewritten as follows:

$$B = bv_1^2 + (bN^* + m)v_1 + m.$$

Thus, $B > 0$ implies that:

$$0 < v_1 = \frac{(bN^* + m) - \sqrt{(bN^* + m)^2 - 4mb}}{2b} < 1.$$

This condition $B > 0$ means that the preys should distribute on the resource patch with a minimum proportion on this patch. In other words, if too many preys remain all the time in the refuge, the predator prey system is unstable. A minimum proportion of preys must stay on the resource patch to ensure stability of the predator prey system.

4. CONCLUSION AND PERSPECTIVES

In Auger et al. (2000) and Chiorino et al. (1999), authors studied quite similar models but using logistic growth for preys also in a system of two patches, a prey refuge and

a common patch for preys and predators. In Chiorino et al. (1999), authors study three models with different prey migration rates, say k and k' from patches 1 to 2 and inversely. The three cases are the following:

1. k and k' are constant.
2. $k = \alpha P$ and k' is constant.
3. $k = \alpha P$ and $k' = \alpha' N_1$,

α and α' are positive constants. They obtained the next results:

1. The aggregated model is equivalent to the local one. In that case, the refuge has few effects on the global dynamics.
2. Exclusion or coexistence. In this model, exclusion means predator extinction and preys density tending to a carrying capacity. However, the authors have shown that the stability of the predator-prey system is more likely to occur in the case of a refuge.
3. Possibility of a limit cycle.

In Auger et al. (2000), authors studied the case where k is constant and $k' = \alpha P^2$, and obtained different results according to parameter values.

In these previous studies, the existence of a prey refuge coupled to predator density dependent migration of preys is more likely to favor global stability of the predator-prey system. In other studies not using aggregation methods nor various scales of time (González-Olivares and Ramos-Jilibert, 2003; Křivan, 1998; Yakubu, 1997), it is also shown that a refuge site for the prey has a stabilizing effect on the system. In this work, we also found that the predator repulsive effect on the prey migration rate have a stabilizing effect on the system, while the prey density dependent migration of preys can destabilize it.

In a future work, we want to study a predator prey model in a system of three patches, a refuge for the prey, a resource patch and a refuge for the predator. It would be interesting to incorporate prey density dependent migration of predators as well as predator dependent migration of preys as we considered in this manuscript. It is also important to extend our model to the case of a $1D$ linear network of N patches ($N \geq 3$) and also to a $2D$ square lattice of patches connected by individual migrations.

APPENDIX

Model I

• For the aggregated model (2.4), the jacobian matrix near the equilibrium point $(0, 0)$ reads as follows:

$$\text{Jac}(0, 0) = \begin{bmatrix} r & 0 \\ 0 & -\mu \end{bmatrix}$$

then we have two real eigenvalues:

$$\lambda_1 = r > 0 \quad \text{and} \quad \lambda_2 = -\mu < 0.$$

Therefore, the equilibrium point $(0, 0)$ is a saddle point.

• At the equilibrium point (N^*, P^*) given by (2.5), the jacobian matrix reads as follows:

$$\text{Jac}(N^*, P^*) = \frac{1}{\alpha + \beta P^*} \begin{bmatrix} 0 & -(\alpha\alpha + m\beta)N^* \\ b\alpha P^* & -\mu\beta P^* \end{bmatrix}$$

Let us set

$$\Delta := \frac{1}{(\alpha + \beta P^*)^2} [(\mu\beta P^*)^2 - 4rb(\alpha)^2 N^*],$$

and

$$A := \frac{\mu\beta P^*}{\alpha + \beta P^*} > 0.$$

Thus:

◦ If $\Delta > 0$ then we obtain two negative real eigenvalues:

$$\lambda_1 = \frac{-A - \sqrt{\Delta}}{2} < 0 \quad \text{and} \quad \lambda_2 = \frac{-A + \sqrt{\Delta}}{2} < 0,$$

and in this case (N^*, P^*) is a stable node.

◦ If $\Delta < 0$ then we obtain two complex eigenvalues with negative real parts:

$$\lambda_1 = \frac{-A - i\sqrt{-\Delta}}{2} \quad \text{and} \quad \lambda_2 = \frac{-A + i\sqrt{-\Delta}}{2},$$

and in this case (N^*, P^*) is a stable focus.

Model II

• The jacobian matrix of system (2.7), at the equilibrium (N^*, P^*) given by (2.8), reads as follows:

$$\text{Jac}(N^*, P^*) = \begin{bmatrix} \frac{m\beta P^*}{\alpha N^* + \beta P^*} & \frac{-r\alpha N^{*2}}{P^*(\alpha N^* + \beta P^*)} \\ \frac{\mu P^*(\alpha N^* + 2\beta P^*)}{N^*(\alpha N^* + \beta P^*)} & -\mu + \frac{\mu^2}{bN^{*2}} \end{bmatrix}$$

Let us set

$$\Delta' := B^2 - 4C,$$

where B is given by (2.9) and $C := \frac{r\alpha\mu N^*(\alpha N^* + 2\beta P^*)}{(\alpha N^* + \beta P^*)^2}$. Thus:

◦ If $\Delta' > 0$ then we obtain two real eigenvalues: $\lambda_1 = \frac{-B - \sqrt{\Delta'}}{2}$ and $\lambda_2 = \frac{-B + \sqrt{\Delta'}}{2}$.

◦ If $\Delta' < 0$ then we obtain two complex eigenvalues: $\lambda_1 = \frac{-B - i\sqrt{-\Delta'}}{2}$ and $\lambda_2 = \frac{-B + i\sqrt{-\Delta'}}{2}$.

• So, for the stability of the equilibrium point, we have:

◦ If $B > 0$, then 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 (node or focus).

- If $B < 0$, then 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.
- If $B = 0$, then the linearization of the aggregated model says that the equilibrium point (N^*, P^*) is a center.

• Now, we are going to demonstrate that the aggregated model (2.7) cannot have closed orbits by use of the negative *Dulac's criterion* (see Arrowsmith and Place, 1992; Edelstein-Keshet, 1998). 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:

$$F(N, P) := \frac{\dot{N}}{\left(\frac{P \cdot N^2}{\alpha N + \beta P}\right)} \quad \text{and} \quad G(N, P) := \frac{\dot{P}}{\left(\frac{P \cdot N^2}{\alpha N + \beta P}\right)},$$

then, we get:

$$F(N, P) := \frac{r\alpha}{P} - a\alpha - \frac{m\beta}{N}$$

and

$$G(N, P) := \frac{-\alpha\mu}{N} + b\alpha - \frac{\mu\beta P}{N^2}.$$

So, we have:

$$\frac{\partial F}{\partial N} = \frac{m\beta}{N^2} \quad \text{and} \quad \frac{\partial G}{\partial P} = \frac{-\beta\mu}{N^2}.$$

As the expression $\frac{\partial F}{\partial n} + \frac{\partial G}{\partial p} = (m - \mu)\frac{\beta}{N^2}$ does not change sign in the connected domain D , and by using the *Dulac's criterion*, we can conclude that when $B \neq 0$ (B is given by (2.9)) then there is no closed orbit. More precisely, when $B > 0$, the equilibrium (N^*, P^*) is globally asymptotically stable while when $B < 0$, this equilibrium is globally asymptotically unstable.

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