

Predator density-dependent prey dispersal in a patchy environment with a refuge for the prey

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In this article, we examine a two-patch predator–prey model which incorporates a refuge for the prey. We suppose that prey migration is dependent on predator density, according to a general function. We consider two different time scales in the dynamics of the model, a fast one describing patch to patch migration, and a slow one involving local prey and predator interaction. We take advantage of the time scales to reduce the dimension of the model by use of methods of aggregation of variables, and thereby examine the effect of predator density-dependent migration of prey on the stability of the predator–prey system. We establish a simple criterion of viability, namely, the existence of a positive and globally stable equilibrium, and show that density dependence has beneficial effects on both species by providing larger equilibrium densities.

Introduction

Predator–prey theory has long been and remains a dominant and important theme in ecology and mathematical ecology, for which many problems remain open.¹ Considered since the first Lotka–Volterra model as a classical application of mathematics in biology, models based on differential equations for interactions between species, thanks to analytical techniques and computerization, have become progressively more complex. They increasingly give a more realistic description of ecological systems, and thereby have improved our understanding of the dynamic relationship between prey and predator. The hiding behaviour of prey in particular has been incorporated as an important ingredient of predator–prey systems² and its consequences on stability have been studied in several models. The traditional way in which refuge has been introduced is via a ‘snapshot’ approach, requiring that a constant proportion or number of prey cannot be killed by the predators.³ Some early theoretical work suggests that the use of refuges by prey, according to this approach, has a stabilizing effect on predator–prey dynamics,^{4–6} whereas other models show no such simple pattern.^{7,8}

More recently, several studies have taken into account the dynamic nature of the refuge, and more generally, the importance of spatial heterogeneity,^{9,10} using patchy environment in their models.^{11–13} The behavioural aspect of this kind of migration focuses on its possible modalities. The density dependence of dispersal has been studied in many papers, whereas the dependence of predator density in prey migration^{13,14} is relatively less studied than the dependence of prey density in predator migration.^{15–18} Spatial heterogeneity leads to the consideration of two different types of dynamics – local interactions between species, on the one hand, and migrations from patch to patch on the other. In some cases, there exist two different time scales (for instance, a fast time scale corresponding to individual processes like migration, and a slow one for demographic changes (see ref. 14); it is then possible to reduce, via results

provided by geometrical singular perturbation (GSP) theory, the dimension of the mathematical model to obtain a reduced or ‘aggregated’ model which can be handled analytically).^{19–21} It has been shown¹¹ by using these methods that the refuge has a stabilizing effect on the equilibrium for a simple Lotka–Volterra model with refuge and density-independent migration. The purpose of this article is to examine the impact of predator density on the migration of prey in such a model. We add here the idea that, to survive, prey has to search for resources outside its refuge and so exposes itself to predation.

We first describe the predator–prey model, comprising a set of three ordinary differential equations governing the local dynamics of prey and predator population densities. These dynamics present two time scales, which enables us to use aggregation of variables methods, based on perturbation techniques and on application of a centre manifold theorem of Fenichel²⁶ to reduce the model to an aggregated one that consists of two equations. To evaluate the impact of density dependence in general, our model also uses a general predator density-dependent function for prey migration. We then study this model and its equilibrium points, and find a simple criterion of stability for a positive equilibrium, depending on various parameters and on the density-dependent migration function. The stability analysis of the non-trivial equilibrium point so found is then considered with a discussion of the results and their ecological interpretations.

The predator–prey model

The model considers two patches, 1 and 2. The prey can move on both patches whereas the predator remains on patch 1. Patch 2, therefore, is a refuge for the prey. Let us denote $n_i(t)$ as the density of the prey at time t on patch i ($i = 1, 2$) and $p(t)$ the density of the predator at time t on patch 1.

We assume that there are two different time scales of the associated dynamics. Migrations are considered to be fast compared to predator–prey interactions. In the prey equations, the dynamics on patch 1 (conversely 2) is represented by a positive (conversely negative) term describing the natural growth (conversely mortality, as there are no resources in the refuge) and a negative term representing prey killed by predators on patch 1. For the predator, we consider a constant natural mortality rate and assume that growth is proportional to the density of prey captured.

The complete system, composed of a set of three ordinary differential equations, is described as follows:

$$\begin{cases} \frac{dn_1}{d\tau} = (kn_2 - \tilde{k}(p)n_1) + \varepsilon n_1(r_1 - ap) \\ \frac{dn_2}{d\tau} = \tilde{} \\ \frac{dp}{d\tau} = \tilde{} \end{cases}$$

The term $r_1 > 0$ represents the intrinsic growth rate of the prey population in patch 1. Terms r_2 and μ are natural mortality rate for prey in patch 2 and for predator in patch 1, respectively. The

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$$\text{As } \text{div}(\tilde{X}) - \frac{f(p)^2 r_1}{pK_1} + bf'(p) < 0 \text{ on } D, \text{ by definition of}$$

the curve Γ , the right-hand part of Equation (5) is reduced to an integral along the transverse section. The sign of that expression is that of $P(h_0) - h_0$, which gives the result. We have therefore shown that the trajectory always progresses towards the inside and so is included in a compact (delimited by Γ). In such a compact, we now show that the trajectory can converge only to the equilibrium point. Using the Poincaré-Bendixson theorem (which describes precisely all possible kinds of trajectories of a plane dynamical system – see refs 22 and 23 for details and demonstration), and because the compact considered contains only one singular point, there can be only two kinds of behaviour:

- The ω -limit set $\omega(x_0)$ (which is the set of accumulation points of the trajectory) is a single point \bar{x} , which is an equilibrium point; the flow of the differential equation $\Phi(t, x_0)$ tends towards \bar{x} as $t \rightarrow \infty$
- ω is a periodic orbit.

Moreover, we have shown previously that as $\text{div}(\tilde{X}) < 0$, there cannot be any periodic orbit (this result is known as the Dulac criterion (see ref. 29), which gives a criterion of non-existence of periodic orbit for a plane dynamical system). Consequently, $\omega(x_0)$ is reduced to a single point and we reach the conclusion: (n^*, p^*) is globally asymptotically stable.

Discussion and conclusion

We have shown that for $\varepsilon < 1$, we were able to reduce the 3-dimension initial system to a 2-dimension aggregated model which presents two general behaviours, depending on the sign of the parameter λ :

If $\lambda < 0$, then the system is not viable. $(0, 0)$ is globally asymptotically stable. The same result applies for $\lambda = 0$, because the predators are then extinct.

If $\lambda > 0$, there is a non-trivial globally asymptotically stable point.

This result can easily be interpreted: the sign of λ depends on the quotient of two quantities $k/k(0)$ and r_1/r_2 , the first denoting the quotient between the migration terms when there are predators, and the second the quotient between the terms of global growth. When there are no predators, if the migration from patch 1 to patch 2 is too important, the prey population naturally disappears as patch 2 is hostile. Note that the influence of k on the qualitative behaviour of the system is determined only by its value for $p = 0$. This result shows that the degree of predator-density dependence of prey dispersal has no influence on stability, whereas in ref. 17, prey-density dependence of predator dispersal could destabilize as the degree of density dependence increases.

We now want to compare the case of density-independent migrations with the case of density-dependent migrations. The density-independent case was studied in a previous paper.¹¹ In this article, we obtained a similar result of global stability of a unique positive equilibrium for the aggregated model. Now, let us focus on prey and predator equilibrium densities.

We return to the predator-density-dependent migration rate of prey. A particular function is the following:

$$\tilde{k}(p) = \alpha_0 + \frac{\alpha p}{D + p}$$

In a more general way, we can write this as follows:

$$\tilde{k}(p) = \alpha_0 + h(p)$$

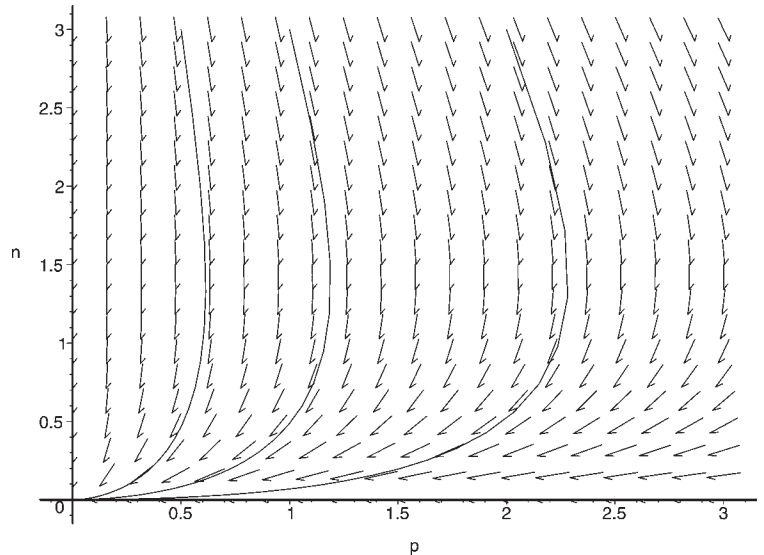


Fig. 1. Phase portrait when $\lambda < 0$, with the following parameter values: $\alpha = 2, D = 5, \alpha_0 = 5, r_1 = 1, r_2 = 4, a = 2, b = 3, \mu = 2, k = 5$.

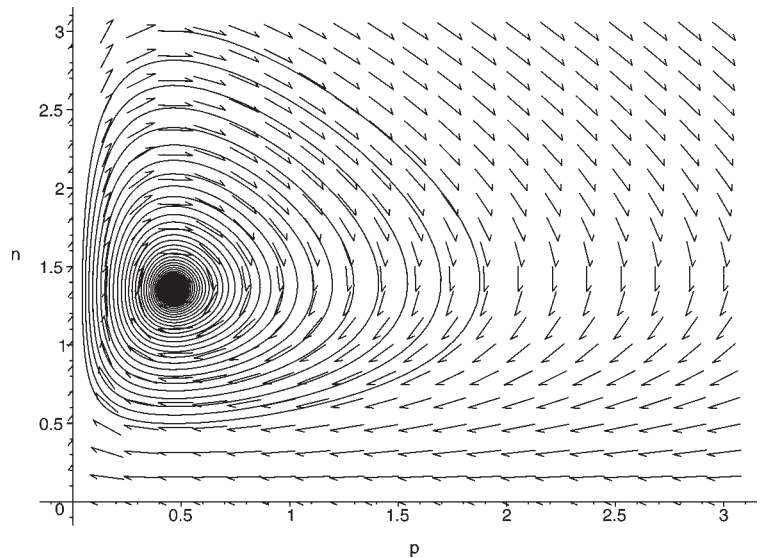


Fig. 2. Phase portrait when $\lambda > 0$, with the following parameter values: $\alpha = 2, D = 5, \alpha_0 = 5, r_1 = 3, r_2 = 2, a = 2, b = 3, \mu = 2, k = 5$.

where $h(p)$ is a strictly positive and increasing function for any $p > 0$ with $h(0) = 0$. The density-dependent migration rate is then the sum of two terms, a constant term α_0 and the density-dependent term $h(p)$. Therefore, we can consider two cases, the density-independent case where $\tilde{k}(p) = \alpha_0$, and the density-dependent case where $\tilde{k}(p) = \alpha_0 + h(p)$.

In both cases, the positive equilibrium (n^*, p^*) is given by the following expressions:

$$n^* = \frac{\mu}{bf(p^*)}$$

and

$$p^* = \frac{r_1}{a} + r_2$$

where $f(p^*)$ represents the prey proportion on patch 1 at the fast equilibrium for the positive equilibrium (n^*, p^*) of the aggregated model.

Let us denote respectively (n_1^*, n_2^*) and (n_d^*, n_d^*) the equilibrium in the density-independent and the density-dependent cases.



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We now identify the terms of order (ϵ) in both formulae, which gives

with

We finally obtain the following aggregated model:

Appendix A

Given that the n -isocline $\frac{\mu}{bk}(k + \tilde{k}(p))$ is always positive for $p > 0$, there exists a unique positive equilibrium point if and only if the equation

$$\frac{k}{k + \tilde{k}(p)}(r_1 + r_2 - ap) - r_2 = 0 \iff kr_1 - \tilde{k}(p)r_2 - kap = 0$$

admits a positive root. Let us denote

$$F(p) = kr_1 - \tilde{k}(p)r_2 - kap$$

Since $F(p)$ is decreasing and $F(p) \rightarrow -\infty$ as $p \rightarrow \infty$, there exists a positive root if and only if $F(0) > 0$. In other words, the parameter $\lambda = kr_1 - \tilde{k}(0)r_2$ must be positive.

Here, we see that if $p = 0$, for $n \neq 0$, $\dot{n} = 0$ if and only if $n = \frac{k + \tilde{k}(0)}{bk\tilde{k}(0)}(u - kr_2)$, so the non-isolated singularities along the n -axis disappear with this development, and another positive equilibrium can appear. Since the case $\lambda = 0$ is minor and more complex, we will not take it further in this study and this article.

Appendix C

If it exists, the non-trivial equilibrium point (n^*, p^*) verifies

Appendix B

Let us rewrite the system (1) the following equivalent way:

$$\begin{cases} \frac{dn_1}{d\tau} = (k(n - n_1) - \tilde{k}(p)n_1) + \epsilon n_1(r_1 - ap) \\ \frac{dp}{d\tau} = \epsilon [\end{cases}$$

The Jacobian matrix associated with the system is

To get a first-order approximation of the manifold, the method consists in writing

Since

and replacing n_1 by this expression in (6). In particular, we obtain

we then have

We can also consider $\frac{dn_1}{dr}$ as

which gives, since $n_1^* = f(p)n$,