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Macroscopic Dynamic Effects of Migrations in Patchy Predator-prey Systems

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Different mechanisms at the behavioural or physiological levels determine many properties of predator-prey systems at the population level. In this paper, we present a method of obtaining complex predator-prey dynamic models from models at a detailed, behavioural level of description. We consider a multi-patch predator-prey model, the dynamics of which contains two time-scales: a fast one, associated with migrations between patches, and a slow one, on which interactions, reproduction and mortality occur. We use methods of perturbation theory in order to aggregate the multi-patch system into a reduced system of two differential equations for the total prey and predator populations. Several models for the aggregated systems are obtained from specific migration scenarios. At the global level, complex expressions for the functional and numerical responses emerge from simple models at the local and behavioural levels. We show that, even if the predator growth rate is directly related to prey deaths at the local level, this may no longer be true at the global level. As a consequence, the coupling between the predator and prey equations may be broken when a predator-prey model is derived from behavioural considerations.

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1. Introduction

The dynamics of predator-prey systems with overlapping generations is usually described by models of the following general form:

$$\frac{dN}{dt} = f(N)N - g(N, P)P, \tag{1a}$$

$$\frac{dP}{dt} = eg(N, P)P - \mu P, \tag{1b}$$

where N and P represent the density of prey and predators, t is the time, $f(N)N$ the prey growth rate in the absence of predation, $g(N, P)P$ the impact of the predator on the prey growth rate, e the conversion efficiency, and μ the per capita death rate of predators. The idea hidden behind the form of eqns (1) is that the predator numerical response, $eg(N, P)$ in (1b), is proportional to $g(N, P)$, the impact of an average predator on the prey growth rate. Moreover, if $g(N, P)$ is interpreted as the number of prey killed per predator in a unit time (hereafter called the *predator ration*), the form of (1) imposes that the only influence of predators on prey is by killing them and

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that the predator growth rate is proportional to the amount of prey killed.

In models of type (1), the predator ration may be identified with the per capita predator impact on the prey population and is usually called the *functional response*. As we will see later, this identification is not always justified for predator-prey models derived from behavioural mechanisms because such models do not have, in general, the form (1). Therefore, we will later use the terms "predator ration" and "per capita predator impact" rather than "functional response" when referring to the models obtained in this paper.

Within the framework defined by (1), many different models have been suggested. The major difference between models sits in the expression describing the functional response. In models of type (1), the functional response $g(N, P)$ plays the key role since, coupling the two equations, it determines the dynamic properties of the predator-prey system. In the classical Lotka–Volterra model, the functional response is linear, i.e., the feeding rate of each predator individual is assumed to respond proportionally to prey abundance. A large number of more realistic expressions have been suggested in order to take account of behavioural or physiological constraints such as predator saturation, predator interference, etc. [Holling, 1959; Watt, 1959; Ivlev, 1961; Takahashi, 1964; Hassell & Varley, 1969; Rosenzweig, 1971; Hassell & Rogers, 1972; Tostowaryk, 1972; Jost *et al*., 1973; Strebel & Goel, 1973; Gomatam, 1974; Rogers & Hassell, 1974; Beddington, 1975; DeAngelis *et al*., 1975; Real, 1977; Arditi *et al*., 1977, 1978; see Arditi (1979) for comparative tables]. Some of these expressions depend on N only, others depend on both N and P. Most of the authors cited above concentrated their studies on the influence of different mechanisms on the functional response only. As we will see in Section 3, behavioural mechanisms can influence the numerical response also, i.e., the effect of prey consumption on the predator growth rate.

Different kinds of arguments have been used to justify the various models. Some persons will be satisfied with phenomenological or empirical arguments. Others will request that models emerge from the detailed description of behavioural mechanisms. In the present paper, we explore one method of obtaining complex models for the entire prey and predator populations from simpler models at a more detailed, local and behavioural scale of description.

We assume a heterogeneous environment consisting of several patches. Prey and predators migrate between the patches. Some patches may be accessible to both species, others can contain one species only. When both species co-occur, they are assumed to interact. Patches reserved for a single species may be actual refuges (for the prey) or simply states of inactivity (for the predators). For the sake of simplicity, we assume that locally (i.e., in each patch) the dynamics is described in the simplest way: each species increases or decreases exponentially (i.e., according to the Malthus law) in the absence of the other species and trophic interactions are described by the Lotka–Volterra model (i.e., they follow the law of mass action). Thus, we can model complex patterns of behaviour such as prey avoiding predators, predators searching for prey, aggregative or repulsive behaviours within each species, predators entering or leaving states of active searching, of handling the prey, etc. We will show that the way in which these phenomena combine with each other at a behavioural scale will translate into mathematical models of predator-prey systems at the global scale. Population-level complex behaviours, like prey logistic-like growth or predator saturation, will emerge from migrations between patches.

Technically, the full model will be a system of ordinary differential equations for the two species in the several patches. Two time-scales will be considered: a fast one on which migrations between patches occur and a slow one on which interactions, reproduction and mortality take place. We will use methods of perturbation theory in order to aggregate the full system into a reduced system of two differential equations for the total prey and predator populations (Section 2). In general, the relations between the predator and the prey equations at the global scale will be different from those adopted at the local scale; they will be determined by the specific modes of migration between the patches (Section 4). In Section 5, we show how some well-known functional responses can be derived using our formalism.

2. The Method: a Prey-predator Model in a Multi-patch Environment

As mentioned, the two species can migrate between different spatial patches and/or switch from one activity to another. In our formalism, spatial patches and different modes of activity are treated in the same way; therefore we will use the same term "patch" to designate both. For the sake of simplicity, we limit ourselves in this section to the case of two patches for each species. The general case of an arbitrary number of patches will be presented in the next section.

2.1. THE FULL MODEL WITH SUBPOPULATIONS

We assume that predation takes place in patch 1 only. Patch 2 can be seen as a refuge for both prey and predators. Thus, patch 2 can, in reality, consist of separate patches for the prey and the predators. We assume that, in the absence of predators, the prey reproduce (or die) exponentially in each patch and that, in patch 1, predation is of the Lotka–Volterra type. In order to obtain prey self-limited growth which stabilises the global predator-prey dynamics we suppose that the net prey growth (without migration) in patch 2 is negative. This models the situation in which patch 2 is a prey refuge where no food is available: to feed, the prey must go to patch 1, where they risk predation. In addition, we suppose that migrations between patches are much more rapid than the other processes in the system. This system is described by the following set of equations:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = \frac{1}{\epsilon}(m_{12}N_2 - m_{21}N_1) + N_1(r_1 - a_1P_1), \quad (2a)$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = \frac{1}{\epsilon}(m_{21}N_1 - m_{12}N_2) - N_2d_2, \quad (2b)$$

$$\frac{\mathrm{d}P_1}{\mathrm{d}t} = \frac{1}{\epsilon}(n_{12}P_2 - n_{21}P_1) + (e_1a_1N_1 - \mu_1)P_1, \quad (2c)$$

$$\frac{\mathrm{d}P_2}{\mathrm{d}t} = \frac{1}{\epsilon}(n_{21}P_1 - n_{12}P_2) - u_2P_2, \quad (2d)$$

where N_1, P_1, N_2, P_2 are prey and predator densities in patches 1 and 2 respectively, r_1 is the prey intrinsic growth rate in patch 1, d_2 is the prey intrinsic death rate in patch 2, a_1 is the so-called searching efficiency, e_1 the conversion efficiency and μ_i the predator mortality in patch i ($i = 1, 2$). The terms m_{ij} (n_{ij}) describe the rate of migration of prey (predators) from patch j to patch i and may, in general, be functions of N_1, P_1, N_2 and P_2. ϵ is a small parameter and its presence in (2) shows explicitly that the dynamics of migrations is much faster than that of other phenomena like predation, growth, and mortality. Throughout this paper, all parameter values are supposed to be positive.

We assume that each patch is homogeneous and that, within a patch, prey and predators encounter each other at random, following the law of mass action. Heterogeneity is modelled by the presence of several patches. Our model is thus a Lotka–Volterra model in a multi-patch environment.

2.2. AGGREGATED VARIABLES

Frequently, the variables of interest are the total abundances of the populations and not their detailed distribution among the patches. In the model described by (2), the variables of interest are $N = N_1 + N_2$ and $P = P_1 + P_2$ rather than N_1, N_2, P_1, and P_2. When migration is much faster than the other processes, one may expect that the distributions of prey and predators among patches come quickly to an equilibrium. The case (not considered here) in which these distributions do not tend to an equilibrium but to a limit cycle can be treated in a similar way (Poggiale & Auger, 1996). In order to explain the method more clearly, we rewrite (2) in a more convenient form:

$$\frac{\mathrm{d}u_1}{\mathrm{d}t} = \frac{1}{\epsilon}(m_{12}u_2 - m_{21}u_1) + u_1u_2(r_1 + d_2 - a_1v_1P), \quad (3a)$$

$$\frac{\mathrm{d}v_1}{\mathrm{d}t} = \frac{1}{\epsilon}(n_{12}v_2 - n_{21}v_1) - v_1v_2(\mu_1 - \mu_2 - e_1a_1v_1N), \quad (3b)$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (r_1u_1 - d_2u_2 - a_1u_1v_1P)N, \quad (3c)$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = -(\mu_1v_1 + \mu_2v_2 - e_1a_1u_1v_1N)P, \quad (3d)$$

where

$$u_i = \frac{N_i}{N}, \quad i = 1, 2, \quad (4a)$$

and

$$v_i = \frac{P_i}{P}, \quad i = 1, 2. \quad (4b)$$

Thus, eqns (3c) and (3d) describe the evolution of the total populations while (3a) and (3b) describe changes of the distribution between patches. Note that the equations for the total abundances [(3c) and (3d)] do not depend explicitly on the rapid migrations while (3a) and (3b) contain both slow population dynamics and fast migration.

2.3. EQUILIBRIUM OF THE FAST PART OF THE EQUATIONS

In the r.h.s. of (3a) and (3b), the terms that describe migrations are much greater than the others. Neglecting the slow terms gives:

$$\frac{\mathrm{d}u_1}{\mathrm{d}t} = \frac{1}{\epsilon}(m_{12}u_2 - m_{21}u_1), \quad (5a)$$

$$\frac{\mathrm{d}v_1}{\mathrm{d}t} = \frac{1}{\epsilon}(n_{12}v_2 - n_{21}v_1). \quad (5b)$$

At equilibrium we have:

$$u_1^* = \frac{1}{1 + \dfrac{m_{21}(u_1^*, v_1^*, N, P)}{m_{12}(u_1^*, v_1^*, N, P)}}, \quad u_2^* = 1 - u_1^*, \quad (6a)$$

$$v_1^* = \frac{1}{1 + \dfrac{n_{21}(u_1^*, v_1^*, N, P)}{n_{12}(u_1^*, v_1^*, N, P)}}, \quad v_2^* = 1 - v_1^*, \quad (6b)$$

where the asterisks denote the equilibrium solutions. In general, (6) should be further solved to find u_1^* and v_1^* as explicit functions of the total variables N and P, since the migration coefficients m_{ij} and n_{ij} may depend on all variables u_1, v_1, N and P. Note that, once at the equilibrium of the fast part of the dynamics, the patch occupancies, N_i, P_i, become functions of the total variables, N and P, only.

The idea behind the method presented here is therefore that, when migration is much faster than the other processes, one may expect that, at each instant of the slow dynamics, the fast part of the dynamics is at an equilibrium. Then, one may take the solution of the fast part and substitute it into the slow part in order to obtain an aggregated system of equations. In general, the evolution of the aggregated system differs from that of the full system. The error is small for short time periods but, after a long time, it can, in principle, accumulate to an important value. Perturbation theory and, in particular, the Centre Manifold Theorem (see Appendix A) give conditions under which this accumulated error is negligible.

2.4. AGGREGATED SYSTEM

Aggregation methods allow to replace the complete system of four eqns (3) by an aggregated system of two equations for the total prey and predator populations (Auger, 1989; Auger & Roussarie, 1994; Poggiale *et al.*, 1995). The Centre Manifold Theorem warrants that, if the solution of (6) is also an asymptotically stable solution of the linearization of (5) around this solution (i.e., it is hyperbolically stable), one may substitute the solution of (6) into (3c–3d) and, thereby, the full system (3) may be replaced by the reduced system:

$$\frac{dN}{dt} = F_N(N, P), \quad (7a)$$

$$\frac{dP}{dt} = F_P(N, P), \quad (7b)$$

where

$$F_N(N, P) = (r_1 u_1^* - d_2 u_2^* - a_1 u_1^* v_1^* P)N, \quad (8a)$$

$$F_P(N, P) = (e_1 a_1 u_1^* v_1^* N - \mu_1 v_1^* - \mu_2 v_2^*)P. \quad (8b)$$

Remember that u_i^* and v_i^* are functions of N and P. Thus, in general, F_N and F_P will be nonlinear functions of N and P.

According to the Centre Manifold Theorem (see Appendix A), eqns (7) describe the trajectory of prey and predator populations with errors of order ϵ with respect to the initial full system (2). Hereafter, system (7) will be called the aggregated system.

3. Recipe

We present here a recipe that summarises in a concise and general form the method presented in the previous section. This recipe should be followed in order to find the aggregated system from a known scenario of migrations between patches. The number of patches is arbitrary and local predator-prey interactions may be of any form.

(1) Write the full system of detailed equations that describe both migrations between patches and predator-prey interactions within patches. Interspecific interactions within patches may be described by any model; in the examples given in this paper, we used the Lotka–Volterra functional response for the sake of simplicity only.
(2) Look for time-scales in the system. If two different time-scales can be determined, and if the fast one is associated with migrations, proceed to point 3. If there is one time-scale only (i.e. changes of abundances of the subpopulations due to migrations are not much faster that changes due to other processes), then the conditions of the Centre Manifold Theorem are not fulfilled and the method cannot be used.
(3) From the original equations for the full system, write equations for the total variables $N = \Sigma_i N_i$ and $P = \Sigma_i P_i$ and for the occupation frequencies $u_i = N_i/N$ and $v_i = P_i/P$. The equations for the total populations will not depend explicitly on migrations (only slow terms will be present), while the equations for the occupation frequencies will contain both predation and migration terms.
(4) Find the equilibrium solution of the equations for the occupation frequencies, simplified by neglecting the small terms (i.e. terms that describe processes other than migrations). If the solutions (denoted by u_i^* and v_i^*) are hyperbolically stable (i.e., they are asymptotically stable solutions of the linearized equations) then proceed to point 5. Otherwise the conditions of the Centre Manifold Theorem are not fulfilled and the method cannot be used.

(5) Substitute the equilibrium frequencies u_i^* and v_i^* (which are functions of the total variables N and P) into the equations for the total variables found in point 3, in order to obtain the aggregated system:

$$\frac{dN}{dt} = F_N(N, P), \tag{9a}$$

$$\frac{dP}{dt} = F_P(N, P). \tag{9b}$$

(6) Check whether the global variables N and P whose dynamics are described by (9) are always bounded. If yes, the aggregated system has been successfully obtained and can be analysed by proceeding to point 7. If not, after a certain time (of the order $1/\epsilon$) the conditions of the Centre Manifold Theorem may no longer be fulfilled and the method should not be used.

(7) The reduced system (9) can be written in the following general form:

$$\frac{dN}{dt} = f(N)N - G(N, P)P, \tag{10a}$$

$$\frac{dP}{dt} = H(N, P)P - \mu(P)P, \tag{10b}$$

where $f(N)$ is the per capita prey net growth function, $G(N, P)$ is the per capita predator impact on the prey growth rate, $H(N, P)$ is the numerical response of the predator, and $\mu(P)$ is the mortality rate of predators in the absence of prey. The formal definitions of these terms are the following:

$$f(N)N = F_N(N, 0), \tag{11a}$$

$$G(N, P)P = F_N(N, 0) - F_N(N, P), \tag{11b}$$

$$\mu(P)P = -F_P(0, P), \tag{11c}$$

$$H(N, P)P = F_P(N, P) - F_P(0, P). \tag{11d}$$

(8) If local predator rations (the amount of prey killed per predator per unit time) are known, the global predator ration for the aggregated system is simply given by

$$g(N, P) = \sum_{i=1}^{n} g_i(N_i^*, P_i^*)v_i^*, \tag{12}$$

where $N_i^* = u_i^* N$, $P_i^* = v_i^* P$, and $g_i(N_i, P_i)$ is the local predator ration in patch i. In general, the global ration $g(N, P)$ will be different from the impact function $G(N, P)$.

4. Migrations and Predator-prey Dynamic Models

A number of different behavioural mechanisms influencing the population dynamics of predator-prey systems can be considered [see Berryman (1981, chapter 5) for a discussion of different migration scenarios]. For example, individuals may have repulsive or aggregative tendencies. Prey may avoid forming aggregates that could be easily detected by potential predators or, on the contrary, prey may aggregate in order to form groups that are easier to defend. Predators may look for the prey and aggregate where the prey are. Or they can avoid competing predators. Finally, predators may be busy handling the prey caught. All these behaviours can be easily translated as models of the migration rates between different patches. It will then be easy to find the population dynamics resulting from a given migration scenario.

Below, we present three examples in which simple migration scenarios result in different mathematical models of predator-prey systems. In all these examples, both prey and predator species can migrate between two patches and predation occurs in patch 1 only. The full system of dynamic equations is given by (2) and the examples differ only in the rates of migration, m_{ij} and n_{ij}. In this section we assume that the migration rates m_{ij} and n_{ij} depend only on the local densities N_j and P_j, i.e., individuals have no knowledge of the situation in the other patches. The aggregated systems were obtained by following the recipe of Section 3.

4.1. Example 1: Prey Avoid Aggregation and Predators Are Retained by Prey

Let prey migrate from patch 2 to patch 1 randomly at a constant rate α and from patch 1 to patch 2 at a rate proportional to N_1, the prey density in patch 1, i.e., prey avoid aggregation in places where they are available to predators. Let predators migrate randomly to patch 1 at a constant rate γ and be retained in patch 1 proportionally to N_1, the prey density in patch 1, i.e., their migration to patch 2 is inversely proportional to N_1. The full dynamics of the system is described by (2) with

$$m_{12} = \alpha, \quad n_{12} = \gamma,$$

$$m_{21} = \beta N_1, \quad n_{21} = \frac{\delta}{N_1}. \tag{13}$$

With this migration scenario, one can easily calculate the equilibrium frequencies, u_1^* and v_1^* [eqns (6)] and prove that the equilibrium is hyperbolically stable. The dynamics of the aggregated system is given by

(10), where

$$\mu = \mu_2 \tag{14}$$

is the natural mortality rate, and

$$G(N) = \frac{4a_1\alpha^2\gamma N^2}{(\alpha + \sqrt{\alpha^2 + 4\alpha\beta N})(\alpha\delta + \delta\sqrt{\alpha^2 + 4\alpha\beta N} + 2\alpha\gamma N)} \tag{15}$$

is the per capita predator impact. The numerical response is

$$H(N) = \left(e_1 - (\mu_1 - \mu_2)\frac{\alpha + \sqrt{\alpha^2 + 4\alpha\beta N}}{2a_1\alpha N}\right)G(N), \tag{16}$$

and

$$f(N) = r(N)\left(1 - \frac{N}{K}\right) \tag{17}$$

is the net per capita prey growth function with

$$r(N) = \frac{2\alpha r_1(r_1 + d_2)}{2d_2\beta N + (r_1 + d_2)(\alpha + \sqrt{\alpha^2 + 4\alpha\beta N})} \tag{18a}$$

and

$$K = \frac{\alpha r_1(r_1 + d_2)}{\beta d_2^2}. \tag{18b}$$

The prey growth (17) has a logistic-like form, which results from the self-repulsive prey behaviour in the favourable patch (Auger & Poggiale, 1996). The migration rate $m_{21} = \beta N_1$ means that, even if predators are absent, overcrowding of prey in patch 1 forces the prey to move to patch 1 where they can only die. Consequently, in the absence of predators, the global prey density converges to a constant value given by (18b). This implies that the global density of prey (and hence that of predators as well) is bounded and, thus, according to the Centre Manifold Theorem, the time evolution of the aggregated system (10), and (14–18) is always close to the time evolution of the full system (2, 13).

In this example, the global predator ration g is equal to the per capita predator impact G given by (15). Thus, the global predator ration (the amount of prey eaten by an average predator in a unit time) is not proportional to the total prey density N (as the local Lotka–Volterra functional response in patch 1) but it behaves like $\sqrt{N}$ for large N. This example shows that density-dependent migrations modify the global predator ration, which differs from that at the local scale.

Note that, contrary to the usual form of predator-prey models (1), the numerical response (16) is not proportional to the predator impact (15), i.e., the relation between the two responses is not given by a constant multiplier but by a complex function of prey density. Figure 1 shows the qualitative behaviour of $G(N)$ and $H(N)$. At low and high prey densities these functions are approximated by:

$$\left.\begin{aligned} G(N) &\approx \frac{a_1\gamma}{\delta}N^2, \\ H(N) &\approx e_1 G(N) - \frac{(\mu_1 - \mu_2)\gamma}{\delta}N, \end{aligned}\right\} \text{for small } N \tag{19}$$

and

$$\left.\begin{aligned} G(N) &\approx a_1\left(\frac{\alpha}{2\beta} + \frac{\delta}{\gamma} + \sqrt{\frac{\alpha}{\beta}N}\right), \\ H(N) &\approx e_1 G(N) - (\mu_1 - \mu_2). \end{aligned}\right\} \text{for large } N \tag{20}$$

The shape of $G(N)$ in Fig. 1 reminds that of the Holling type III functional response. The acceleration phase at low density, where an increase in prey density leads to more-than-linear increase in $G(N)$, is due to the assumption that predators are retained by the prey in patch 1. However, as the numerical response $H(N)$ is not proportional to $G(N)$, the latter cannot be strictly identified with the functional response used in models of type (1). Nevertheless, if the prey density is high, one can see from (20) that the numerical response $H(N)$ becomes proportional to $G(N)$. For large N, the system (1) becomes therefore a valid approximation for the aggregated populations and $G(N)$ in (20) can be used for the functional response $g(N)$ of (1).

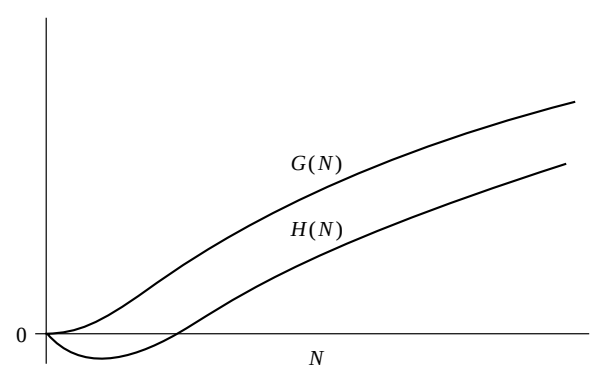

FIG. 1. Qualitative behaviour of the functions $G(N)$ and $H(N)$ of example 1. The predator mortality in patch 1, μ_1, is assumed to be higher than that in patch 2, μ_2.

In the present example, even though the local numerical response in patch 1 is proportional to the local predator impact in the same patch, the proportionality is lost at the global level. In fact, the prey influence the predator growth rate not only by supplying food but also by forcing predators to migrate to a patch where their mortality is different. This results in a decoupling of the numerical response from the predator impact and, consequently, in a decoupling between the predator and the prey equations: the form (1) is broken.

4.2. EXAMPLE 2: PREY AVOID AGGREGATION AND PREDATORS

Let the prey migrate from patch 2 to patch 1 randomly at a constant rate α and from patch 1 to patch 2 at a rate which is the sum of a term proportional to the prey density in patch 1 and of a term proportional to the predator density in the same patch. This means that prey avoid to aggregate in places where they are available to predators (as in the previous example) and flee the predators by going back to the refuge (patch 2). Let predators migrate randomly. The full dynamics of the system is described by (2) with

$$m_{12} = \alpha, \quad n_{12} = \gamma,$$
$$m_{21} = \beta N_1 + \lambda P_1, \quad n_{21} = \sigma. \tag{21}$$

Again, one can easily find the equilibrium (u_1^*, v_1^*) and verify that it is hyperbolically stable. The aggregated system is given by (10) with

$f(N)$ given again by (17), and

$$\mu = (\mu_1 v_1^* + \mu_2(1 - v_1^*)), \tag{22}$$

where

$$v_1^* = \frac{\gamma}{\gamma + \sigma}. \tag{23}$$

In order to shorten mathematical expressions that will follow, we define the function

$$D(N, P) = \sqrt{(\alpha + \lambda v_1^* P)^2 + 4\alpha\beta N}. \tag{24}$$

Then, the global predation ration is given by

$$g(N, P) = \frac{2\alpha a_1 v_1^* N}{\alpha + \lambda v_1^* P + D(N, P)}, \tag{25}$$

the per capita predator impact on the prey growth rate is

$$G(N, P) = g(N, P) + \frac{(r_1 + d_2)\lambda v_1^*}{2\beta}\left(1 - \frac{\lambda v_1^* P + 2\alpha}{D(N, P) + D(N, 0)}\right), \tag{26}$$

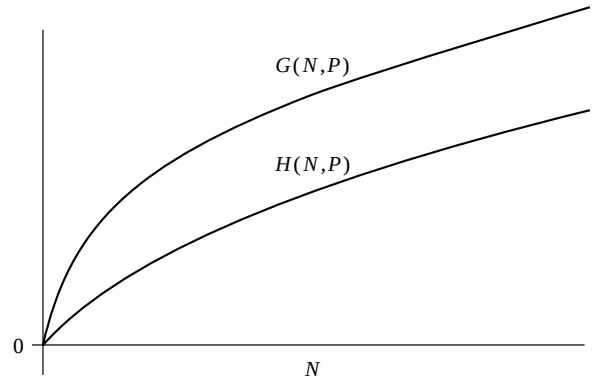

FIG. 2. Qualitative behaviour of the functions $G(N, P)$ and $H(N, P)$ of example 2. The predator density, P, is fixed at a constant value.

and the numerical response is given by

$$H(N, P) = e_1 g(N, P). \tag{27}$$

Due to prey self-limitation (in the same way as in the previous example) and to the fact that predators can only harm prey, both N and P are bounded and thus, according to the Centre Manifold Theorem, the aggregated system (10) and (22–27) approximates the full system (2) and (21) with no time limit.

Figure 2 shows the qualitative behaviour of $G(N, P)$ and $H(N, P)$ for a fixed predator density P. Note that both functions start from the same value for $N = 0$ but with different slopes, whereas, for large N they have the same slopes but differ from each other by a constant. At low and high prey densities they are approximated by:

$$\left.\begin{aligned} G(N, P) &\approx \frac{1}{e_1} H(N, P) + \frac{(r_1 + d_2)\lambda v_1^*}{\lambda v_1^* P + \alpha} N, \\ H(N, P) &\approx e_1 \frac{a_1 \alpha v_1^* N}{\alpha + \lambda v_1^* P}, \end{aligned}\right\} \quad \text{for small } N \ (P \text{ fixed}) \tag{28}$$

and

$$\left.\begin{aligned} G(N, P) &\approx \frac{1}{e_1} H(N, P) + \frac{v_1^*(r_1 + d_2)\lambda}{2\beta}, \\ H(N, P) &\approx e_1 v_1^* \left(a_1 \sqrt{\frac{\alpha}{\beta}} \sqrt{N} - \frac{\alpha + v_1^* \lambda P}{2\beta}\right). \end{aligned}\right\} \quad \text{for large } N \ (P \text{ fixed}) \tag{29}$$

At low and high predator densities these functions are

approximated by:

$$\left.\begin{aligned} G(N,P) &\approx \frac{1}{e_1}H(N,P) + \frac{(r_1+d_2)\lambda v_1^*}{2\beta} \\ &\quad\times\left(1-\frac{\alpha}{D(N,0)}-\frac{2\alpha\beta\lambda v_1^* NP}{(D(N,0))^3}\right), \\ H(N,P) &\approx \frac{2e_1a_1\alpha v_1^* N}{\alpha+D(N,0)}\left(1-\frac{\lambda v_1^*}{D(N,0)}P\right). \end{aligned}\right\} \quad \text{for small } P \ (N \text{ fixed}) \tag{30}$$

and

$$\left.\begin{aligned} G(N,P) &\approx \frac{1}{e_1}H(N,P), \\ H(N,P) &\approx \frac{e_1a_1\alpha}{\lambda}\frac{N}{P}. \end{aligned}\right\} \text{for large } P \ (N \text{ fixed}) \tag{31}$$

Commonly, the per capita predator impact on the prey growth rate is supposed to be proportional to the predator ration [as in (1)]. In the present example this is not the case. The per capita predator impact (26) is the sum of the predator ration, which describes predation, and a term proportional to $(r_1 + d_2)$ which describes modifications of the prey growth rate due to changes of prey behaviour in the presence of predators. In a heterogeneous environment the predator can influence the prey growth rate not only by killing the prey, but also by increasing their migration to less favourable places. This results in decoupling between the prey and the predator equations. Nevertheless, if the prey or predator density is high (the other density being fixed), one can see from (29) or (31) that the numerical response $H(N, P)$ becomes proportional to $G(N, P)$.

Note that if $\lambda = 0$, i.e., if the migrations are described by

$$m_{12} = \alpha, \quad n_{12} = \gamma,$$
$$m_{21} = \beta N_1, \quad n_{21} = \sigma. \tag{32}$$

then, as seen from (26) and (27), the per capita predator impact on prey growth is proportional to the numerical response. If $\lambda > 0$ and $\beta = 0$, i.e., if the migrations are described by

$$m_{12} = \alpha, \quad n_{12} = \gamma,$$
$$m_{21} = \lambda P_1, \quad n_{21} = \sigma. \tag{33}$$

then the per capita predator impact

$$G(N,P) = \left(1 + (r_1+d_2)\frac{\lambda v_1^*}{a_1\alpha}\right)g(N,P) \tag{34}$$

is also proportional to the numerical response (see Appendix B for a proof that, for some values of the parameters, the dynamics of the aggregated system that results from the migration scenario (33) is bounded and, thus, that the Centre Manifold Theorem can be applied without time limitation). With either of the migration scenarios (32) or (33) the resulting aggregated systems are of type (1), i.e., the prey and the predator equations are coupled by the fact that predator growth is proportional to predator impact on the prey. Nevertheless, it would be erroneous to conclude that combining the two scenarios will result also in a system of type (1). Indeed, combining (32) and (33) gives the migration scenario (21), for which the global per capita predator impact (26) is proportional neither to the predator ration (25) nor to the numerical response (27) and, thus, the predator and the prey equations are not coupled. We see here that combining mechanisms does not result in the sum of their separate effects.

4.3. EXAMPLE 3: PREY AVOID AGGREGATION AND PREDATORS, PREDATORS ARE RETAINED BY PREY

In example 1, the per capita predator impact (15) was equal to the predator ration but was decoupled from the numerical response (16); in example 2 the reverse occurred: the numerical response (27) was proportional to the predator ration (25) but the per capita predator impact (26) was decoupled from the predator ration (25). One can expect that combining the migration scenarios (13) and (21) from both examples will result in decoupling both the numerical response and the per capita predator impact from the predator ration. This is indeed the case, but the resulting mathematical formulas are too long to be shown here (probably longer than the rest of the paper). Instead, we present below arguments that these two decouplings occur simultaneously and, moreover, that the numerical response is not proportional to the per capita predator impact.

Let the migration rates be the sum of those from the two previous examples. The full dynamics of the system is described by (2) with

$$m_{12} = \alpha, \quad n_{12} = \gamma,$$
$$m_{21} = \beta N_1 + \lambda P_1, \quad n_{21} = \frac{\delta}{N_1} + \sigma. \tag{35}$$

The system from example 1 [with migration rates

given by (13)] is a special case of (35) with $\lambda = 0$ and $\sigma = 0$. The system from example 2 [with migration rates given by 21] is a special case of (35) with $\delta = 0$. Using these facts and treating the system (2, 35) as a perturbation of systems from examples 1 and 2, one can show (see details in Appendix C) that, in the aggregated system of the system (35), the numerical response is decoupled from the predator ration (as in example 1), that the per capita predator impact is also decoupled from the predator ration (as in example 2) and that the per capita predator impact is decoupled from the numerical response.

5. Some Scenarios Generating Known Functional Responses

Some functional responses used frequently in the ecological literature are known to have been derived from behavioural mechanisms (Holling, 1959; Beddington, 1975). In this section, we show how these mechanisms can be described in our formalism of migrations between patches and how each component of the predator-prey system is affected by these mechanisms. We show also that mechanisms other than those originally proposed lead to the same functional responses. In this section, each patch corresponds to a behavioural mode rather than to a distinct place. In this case, the migration rates (switching rates) may also depend on the total densities: if an individual A switches to another mode when it encounters another individual B, it may do so independently of the behavioural mode of B.

5.1. HOLLING TYPE II FUNCTIONAL RESPONSE

The Holling type II functional response is

$$g(N) = \frac{AN}{1 + BN}. \tag{36}$$

where A and B are positive constants. Holling (1959) obtained this expression by assuming that, after catching a prey, a predator spends some time T_h handling it. In terms of our formalism, this mechanism means that patch 1 only is available to the prey, that predators leave patch 1 at a rate proportional to the prey density ($n_{21} = \varphi N$), and that the rate of their migration from patch 2 to patch 1 is inversely proportional to the handling time ($n_{12} = 1/T_h$). The full dynamics of the system is given by

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f(N)N - a_1 N P_1, \tag{37a}$$

$$\frac{\mathrm{d}P_1}{\mathrm{d}t} = \frac{1}{\epsilon}\left(\frac{1}{T_h}P_2 - \varphi N P_1\right) + (e_1 a_1 N - \mu_1)P_1, \tag{37b}$$

$$\frac{\mathrm{d}P_2}{\mathrm{d}t} = \frac{1}{\epsilon}\left(\varphi N P_1 - \frac{1}{T_h}P_2\right) - \mu_2 P_2, \tag{37c}$$

If one assumes that the migrations between patches (i.e., the switching between the two behavioural modes) are faster than the variations of the total predator and prey populations, the system (37) aggregates into a two-dimensional one. The dynamics of the aggregated system is given by (10) where the predator impact is

$$G(N) = \frac{a_1 N}{1 + \varphi T_h N}, \tag{38}$$

which is equal to the predator ration $g(N)$ and which is formally identical to (36). The numerical response is

$$H(N) = (e_1 + (\mu_1 - \mu_2)\varphi T_h)g(N), \tag{39}$$

the mortality is

$$\mu = \mu_1, \tag{40}$$

and the growth function $f(N)$ is not affected by predator behaviour. If the prey growth is self-limiting (e.g., of the logistic type), then the global prey and predators densities are bounded, and the time evolution of the aggregated system (10) and (38–40) is always close to that of the full system (37). Note that the aggregated system (10) and (38–40) has the "canonical" form (1).

5.2. DEANGELIS-BEDDINGTON FUNCTIONAL RESPONSE

The DeAngelis-Beddington functional response (DeAngelis *et al.*, 1975; Beddington, 1975) includes dependence on predator density in order to reflect mutual interference. It is

$$g(N, P) = \frac{AN}{1 + BN + CP}, \tag{41}$$

where A, B and C are positive constants. Beddington (1975) has proposed a mechanism that results in the functional response (41). This mechanism is the same as that of Holling (see the previous subsection), extended to describe direct interference between predators. After catching a prey, a predator spends

some time T_h handling it (as in Holling's mechanism), and after encountering another predator individual, it wastes some time T_w on direct interference.

Again, it is easy to transpose this mechanism into our formalism. As before, assume that prey exist in patch 1 only. Predators leave patch 1 at a rate which is the sum of a term proportional to the prey density and a term proportional to the total predator density ($n_{21} = \varphi N + \psi P$) and stay in patch 2 while handling prey or interfering with each other. The mean time that a predator spends in patch 2 (i.e., the reciprocal of n_{12}) is the weighted sum of T_h and T_w:

$$T_2 = \frac{\varphi N T_h + \psi P T_w}{\varphi N + \psi P}, \tag{42}$$

The full system is thus

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f(N)N - a_1 N P_1, \tag{43a}$$

$$\frac{\mathrm{d}P_1}{\mathrm{d}t} = \frac{1}{\epsilon}\left(\frac{\varphi N + \psi P}{\varphi N T_h + \psi P T_w} P_2 - (\varphi N + \psi P)P_1\right) + (e_1 a_1 N - \mu_1)P_1, \tag{43b}$$

$$\frac{\mathrm{d}P_2}{\mathrm{d}t} = \frac{1}{\epsilon}\left(\varphi N + \psi P)P_1 - \frac{\varphi N + \psi P}{\varphi N T_h + \psi P T_w} P_2\right) - \mu_2 P_2. \tag{43c}$$

The aggregated system is given by (10) with

$$G(N, P) = \frac{a_1 N}{1 + \varphi T_h N + \psi T_w P}, \tag{44a}$$

$$g(N, P) = G(N, P), \tag{44b}$$

$$H(N, P) = \left(e_1 + \frac{\mu_1 - \mu_2}{1 + \psi T_w P} T_h\right) G(N, P), \tag{44c}$$

$$\mu(P) = \frac{\mu_1 + \mu_2 \psi T_w P}{1 + \psi T_w P}, \tag{44d}$$

and the per capita net growth function $f(N)$ is not affected by predator behaviour. As before, if the prey growth is self-limiting (e.g., of the logistic type), then the global prey and predator densities are bounded, and the time evolution of the aggregated system (10, 44) is always close to that of the full system (43). Note that the numerical response (44c) is not simply obtained from the predator impact (44a) and, consequently, the aggregated predator and prey equations are not coupled. However, if the predator death risk is the same while performing different activities ($\mu_1 = \mu_2$, a rather strong assumption), then $H(N, P)$ is proportional to $G(N, P)$ and the predator and prey equations are coupled. The predator ration (44b) is equal to the impact function (44a) and is formally identical to the DeAngelis-Beddington functional response (41).

The above migration scenario translates accurately the mechanism suggested by Beddington (1975). However, one may object that the number of predators encountered by a predator individual in patch 1 should be proportional to the number of predators in that patch, P_1, rather than to the total number of predators, P. Indeed, one may argue that a predator individual that is handling captured prey or interfering with another predator individual cannot enter into a new interference relation. Moreover, one may take account of the fact that each predator-predator encounter removes not one but two predators from patch 1. Thus, the migration rate from patch 1 to patch 2 should be $n_{21} = \varphi N + 2\psi P_1$ and the migration rate from patch 2 to patch 1 will read:

$$n_{12} = \frac{\varphi N + 2\psi P_1}{\varphi N T_h + 2\psi P_1 T_w}. \tag{45}$$

Consequently, the full system is

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f(N)N - a_1 N P_1, \tag{46a}$$

$$\frac{\mathrm{d}P_1}{\mathrm{d}t} = \frac{1}{\epsilon}\left(\frac{\varphi N + 2\psi P_1}{\varphi N T_h + 2\psi P_1 T_w} P_2 - (\varphi N + 2\psi P_1)P_1\right) + (e_1 a_1 N - \mu_1)P_1, \tag{46b}$$

$$\frac{\mathrm{d}P_2}{\mathrm{d}t} = \frac{1}{\epsilon}\left((\varphi N + 2\psi P_1)P_1 - \frac{\varphi N + 2\psi P_1}{\varphi N T_h + 2\psi P_1 T_w} P_2\right) - \mu_2 P_2, \tag{46c}$$

and the aggregated system is given by (10) with

$$G(N, P) = \frac{aN}{4\psi T_w P}\left(-1 - \varphi T_h N + \sqrt{(1 + \varphi T_h N)^2 + 8\psi T_w P}\right), \tag{47a}$$

$$g(N, P) = G(N, P), \tag{47b}$$

$$H(N, P) = \left(e_1 + \frac{(\mu_1 - \mu_2)\varphi T_h}{1 + \sqrt{1 + 8\psi T_w P}}\left(1 + \frac{2 + \varphi T_h N}{\sqrt{1 + 8\psi T_w P} + \sqrt{(1 + \varphi T_h N)^2 + 8\psi T_w P}}\right)\right) \times G(N, P), \tag{47c}$$

$$\mu(P) = \mu_2 + \frac{2(\mu_1 - \mu_2)}{1 + \sqrt{1 + 8\psi T_w P}}. \tag{47c}$$

Again, the numerical response (47c) is not a function of the per capita predator impact (47a) and the predator and prey equations are not coupled.

An equivalent correction to Beddington's mechanism was made by Ruxton *et al*. (1992) to derive a functional response formally equivalent to (47a) with arguments based on chemical reaction kinetics. Although having a quite different mathematical expression, the function (47a) behaves very similarly to the functional response (41). In particular, both (41) and (47a) have the same limits as $N, P \to 0$ and both saturate at the same value as $N, P \to \infty$. In practical situations, it will be difficult to discriminate between (41) and (47a). For the sake of simplicity, (41) can be used in ecological models.

One can also obtain the functional response (41) from a behavioural mechanism different from that proposed by Beddington. Consider predators having one behavioural mode only (one patch) and prey individuals that waste their time (which would otherwise be devoted to feeding) when they encounter each other (e.g., by fighting) or when they notice a predator (e.g., by fleeing). Such a situation may be described by (2) with

$$m_{12} = \alpha, \quad n_{12} = \gamma,$$
$$m_{21} = \beta N + \lambda P, \quad n_{21} = 0. \tag{48}$$

The aggregated system is given by (10) with

$$f(N) = \frac{r_1 \alpha}{\alpha + \beta N}\left(1 - \frac{d_2 \beta}{r_1 \alpha} N\right), \tag{49a}$$

$$g(N, P) = \frac{a_1 N}{1 + \frac{\beta}{\alpha} N + \frac{\lambda}{\alpha} P}, \tag{49b}$$

$$G(N, P) = \left(1 + \frac{(r_1 + d_2)\lambda}{a_1(\alpha + \beta N)}\right) g(N, P), \tag{49c}$$

$$H(N, P) = g(N, P). \tag{49d}$$

The predator ration (49b) is formally equivalent to the functional response (41). Note that, again, as the numerical response and the per capita predator impact are not simply related, the predator and prey equations of the aggregated system are not coupled. If $\lambda = 0$, the ration (49b) and the impact (49c) reduce both to Holling's functional response (36).

6. Discussion

We have presented a method of constructing a mechanistic model of global predator-grey dynamics if detailed behavioural mechanisms are known. This method allows to aggregate a system of $2n$ ordinary differential equations (in the case of n patches and one prey and one predator species) into a system of two equations for the densities of total prey and predator populations. In general, such aggregated model has no simple mathematical expression. In particular, complex models emerge at the global scale even when prey and predators interact locally in a simple Lotka–Volterra manner. Looking at the qualitative behaviour of the components of these complex models can help find an appropriate phenomenological model or simpler mathematical expressions that approximate the exact ones for some ranges of variable values (e.g., high or low prey density).

We have shown that, even if the predator impact on prey growth is equal to the predator ration (number of prey killed per predator in a unit time) at the local level, this is no longer the case at the global level (examples 2 and 3). This results from the fact that predators can effect the prey growth rate not only by eating them but also by influencing their behaviour. Similarly, the numerical response H may become uncoupled from the predator ration at the global scale as a result of predator migrations depending on prey density (examples 1 and 3). As a consequence, at the global level, the predator growth rate is generally not directly related to prey deaths.

In general, the predator ration $g(N, P)$ differs from the per capita predator impact $G(N, P)$ defined by (11b). The former is the amount of prey eaten per unit time by an average predator in the course of its foraging behaviour (i.e., locally), whereas the latter represents the effect of an average predator on the prey growth rate on the scale of the total population. These two functions are often confounded with one another because in "canonical" models of the form (1), they are identical to each other and are called the functional response. Nevertheless, they are generally distinct: the function $G(N, P)$ describes phenomena at the global level, whereas the function $g(N, P)$ can only be determined at the local level: it does not appear explicitly in the aggregated system (10).

Each migration scenario leads to a global predator ration that differs from that assumed locally. In general, different rations emerge from different scenarios but, as we have seen in Section 5, distinct scenarios may also result in identical or similar rations. In particular, we have showed that some rations that are equivalent to some well-known functional responses emerge from different migration or behavioural mechanisms.

When building predator-prey models, one usually concentrates on the functional response because it plays the key role in determining the dynamic properties of systems of type (1). However, we have shown here that, if the functional response is to be determined from behavioural mechanisms, one should also account for the effect of these mechanisms on other terms. This frequently results in uncoupling of the predator and prey equations, i.e., the form (1) is broken. Consequently, such mechanistically derived functional responses no longer play a central role in this approach to predator-prey theory.

Predator-prey systems are nonlinear: even the simplest one, the Lotka–Volterra model, is described by nonlinear equations. Due to this nonlinearity, mechanisms generally do not add up in a simple way. They interfere and influence each other. In particular, if we know the dynamic properties of a model with a given mechanism, we cannot use this knowledge to predict the properties of another model where the same mechanism is present simultaneously with some others: we have to construct and study the new model from the very beginning. Indeed, in example 2, the migration scenario is the sum of two simpler scenarios; nevertheless, the emerging property (the uncoupling of the prey and predator equations) is new and exists in neither of the two constituent simpler cases. Therefore, one cannot expect that decomposing mechanisms into simpler ones and studying them separately will give a complete understanding of the full predator-prey system.

As was mentioned, the mathematical formalism remains exactly the same if "patch" is replaced by "activity mode" and "migration" is replaced by "switching activities". Therefore, our results and conclusions apply not only to spatially heterogeneous systems but also to a much wider class of behavioural models, in which species can move between patches and/or switch activities.

In the present paper, we have assumed that migrations occurred on a fast time scale and interactions, reproduction and mortality occurred on a slow time-scale. This has enabled us to show how the details of individual behaviour on the fast time-scale determine the population dynamics on the slow time-scale. However, there exist situations in which migrations are slower than the predation process. Indeed, it will be shown in a forthcoming paper (Poggiale, Michalski and Arditi, in preparation) that the alternative hypothesis that predation is fast and that migrations, reproduction and mortality are slow leads to a ratio-dependent functional response in the sense of Arditi & Ginzburg (1989).

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APPENDIX A

The Centre Manifold Theorem

Let X be a C^∞ vector field on $R^{k_1} \times R^{k_2} \times R$. Assume that for each $n \in R^{k_2}$, the point $(u^*(n), n, 0)$ is a fixed point of X. Let $DX(n)$ be the linear part of the vector field at this fixed point. Assume that $DX(n)$ has k_1 eigenvalues with negative real parts. Furthermore, let 0 be an eigenvalue with multiplicity $k_2 + 1$. Then the global space splits into $E_n^s \times E_n^c$ where E_n^s is the stable space such as $\dim(E_n^s) = k_1$ and E_n^c is the centre space with $\dim(E_n^c) = k_2 + 1$. The eigenvalues of $DX(n)$ restricted to the stable space have negative real parts, and zero is the unique eigenvalue of the restriction of $DX(n)$ to the centre space. With these notations, the Centre Manifold Theorem (Fenichel, 1971; Auger & Roussarie, 1994; Chow *et al.*, 1994) can be written in the following form:

Theorem: for each compact $\Delta \subset R^{k_2}$ and for each positive integer K, there exists a positive real ϵ_0 and a C^K-map $\Psi: \Delta \times]-\epsilon_0; \epsilon_0[\to R^{k_1}$, such that:

(*i*) $\Psi(n, 0) = u^*(n)$, *for each* $n \in \Delta$;
(*ii*) *The graph W of Ψ is invariant under the flow of X, and is transversally attractive*;
(*iii*) *W is tangent to E_n^c at each $n \in \Delta$.*

Conclusion (*i*) means that each equilibrium of the vector field X is on W, called the Centre Manifold. Conclusion (*ii*) says that each solution of the global system which starts on W, stays on it as long as $n \in \Delta$, and that each solution of the full system is quickly close to its projection onto the centre manifold W. The last conclusion allows us to treat the dynamics of the full system as perturbation of its projection onto W and to expand it with respect to $\epsilon \in]-\epsilon_0, \epsilon_0[$, if ϵ is small. If the projection onto W is structurally stable, then the perturbation terms of order $O(\epsilon)$ do not influence the qualitative behaviour of the dynamics and one can neglect them.

In our application, R^{k_1} is the space of occupancy frequencies u_1 and v_1, $u^* = (u_1^*, v_1^*)$ is the equilibrium of the fast part of the dynamics, R^{k_2} is the space of global densities N and P, and the real variable ϵ is the small time-scale factor of the model (2). In the case of two populations N and P and two patches we have $k_1 = 2$, $k_2 = 2$ and $n = (N, P)$. The fact that $DX(n)$ has k_1 eigenvalues with negative real parts implies the hyperbolic stability of the fast equilibrium. The eigenvalue 0 with the multiplicity $k_2 + 1$ corresponds to $k_2 + 1$ first integrals of the fast part of the dynamics, in our case N, P, and the constant ϵ. If the global densities, solutions of the restricted dynamics on the Centre Manifold, are bounded then it is possible to find a compact Δ such that each trajectory entering into it remains in its interior forever. In this case, the dynamics of the full system is approximated by its projection onto the Centre Manifold W with an error of order ϵ and without time limitation. In all our examples the aggregated systems were structurally stable, which allowed us to neglect perturbation terms of order $O(\epsilon)$.

APPENDIX B

Global Stability of the Aggregated System of Example 2 with $\beta = 0$ and $\lambda > 0$

We show here that the migration scenario of example 2, with $\beta = 0$ and $\lambda > 0$, i.e., with the migration rates given by

$$m_{12} = \alpha, \quad n_{12} = \gamma,$$
$$m_{21} = \lambda P_1, \quad n_{21} = \sigma, \tag{B.1}$$

leads to a bounded dynamics for some values of the parameters. The aggregated system (found by following the recipe from Section 3) is:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = r_1 N\left(1 - \frac{(r_1 + d_2)\lambda v_1^* P}{r_1(\alpha + \lambda P)} - \frac{a_1 \alpha v_1^* P}{r_1(\alpha + \lambda P)}\right), \tag{B.2a}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = -P\left(\mu_1 v_1^* + \mu_2 v_2^* - \frac{e_1 a_1 v_1^* \alpha N}{\alpha + \lambda P}\right). \tag{B.2b}$$

In order to simplify the study of this system, we define the following parameters:

$$v_1^* = \frac{\gamma}{\sigma+\gamma}, \quad v_2^* = \frac{\sigma}{\sigma+\gamma}, \quad \mu = \mu_1 v_1^* + \mu_2 v_2^*,$$

$$\rho = \frac{\mu}{r_1}, \quad b = \frac{e_1 a_1 v_1^*}{\mu}, \quad A = \frac{r_1 + d_2}{r_1} v_1^*,$$

$$B = \frac{a_1 v_1^* \alpha}{\lambda r_1}, \quad C = A + B, \tag{B.3}$$

and make the following change of variables and time:

$$x = N, \quad y = \lambda P, \quad \theta = r_1 t. \tag{B.4}$$

With these notations, the system (B.2) is equivalent to:

$$\frac{\mathrm{d}x}{\mathrm{d}\theta} = x\left(1 - \frac{Cy}{1+y}\right), \tag{B.5a}$$

$$\frac{\mathrm{d}y}{\mathrm{d}\theta} = -\rho y\left(1 - \frac{bx}{1+y}\right). \tag{B.5b}$$

Now, we use the fact that the trajectories of such a system are not modified if we multiply each equation by the same positive function. We multiply each equation by $1 + y$ to obtain:

$$\frac{\mathrm{d}x}{\mathrm{d}\theta} = x(1 - (C-1)y), \tag{B.6a}$$

$$\frac{\mathrm{d}y}{\mathrm{d}\theta} = -\rho y(1 - bx + y). \tag{B.6b}$$

In order to prove that the solutions of (B.2) are bounded, it is sufficient to prove that the solutions of (B.6) are bounded. (B.6) has a unique equilibrium in the positive orthant:

$$x^* = \frac{C}{b(C-1)}, \tag{B.7a}$$

$$y^* = \frac{1}{C-1}, \tag{B.7b}$$

if $C > 1$, i.e., according to the definitions (B.3), if

$$\lambda d_2 \gamma + a_1 \alpha \gamma > \lambda r_1 \sigma. \tag{B.8}$$

Let us consider the following function:

$$V(x, y) = \rho b(x - x^* - x^* \operatorname{Ln}(x)) + (C-1)(y - y^* - y^* \operatorname{Ln}(y)) \tag{B.9}$$

It is easy to verify that V is a Lyapounov function for the system (B.6) with the minimum at $(x^*; y^*)$. A simple computation shows that:

$$\frac{\mathrm{d}}{\mathrm{d}\theta}(V(x(\theta), y(\theta))) = -\frac{\rho((C-1)y - 1)^2}{C-1}. \tag{B.10}$$

The function V decreases along each trajectory of (B.6) if condition (B.8) is satisfied. Consequently, for certain values of the parameters, all trajectories starting from the positive orthant converge to the positive equilibrium, and thus are bounded. This means that the migration scenario (B.1) according to which prey avoid predators by going to the refuge where their local growth is negative, leads to a globally stable system. The presence of predators in patch 1 is sufficient to prevent an unbounded growth of prey, if prey avoid predators and if condition (B.8) is satisfied.

APPENDIX C

Proofs for Example 3

We show here that the migration scenario from example 3 leads to uncoupling of both the numerical response and the per capita predator impact from the predator ration. In example 3, the migration rates are given by:

$$m_{12} = \alpha, \quad n_{12} = \gamma,$$

$$m_{21} = \beta N_1 + \lambda P_1, \quad n_{21} = \frac{\delta}{N_1} + \sigma. \tag{C.1}$$

Let $p = (\alpha; \beta; \gamma; \delta; \lambda; \sigma) \in R^6$ be the parameter vector, and let $x = (u_1; v_1; p)$. This vector is in $E = (]0; 1[)^2 \times R^6$. We define the map: Ω: $E \to R^2$ such that:

$$\Omega(x) = \begin{pmatrix} \alpha - u_1(\alpha + \beta u_1 N + \lambda v_1 P) \\ \gamma - v_1\left(\gamma + \sigma + \dfrac{\delta}{u_1 N}\right) \end{pmatrix}, \tag{C.2}$$

where N and P are fixed positive parameters. With these notations, finding an equilibrium of (5) (i.e., the fast part of the dynamics) with migration rates given by (C.1) is equivalent to solving the equation:

$$\Omega(x) = 0. \tag{C.3}$$

We are interested in systems where all components of vector p are non negative. We show that the aggregated system (constructed according to the recipe from Section 3) approximates the full system without time limitation and that the predator ratio $g_p(N, P)$, the numerical response $H_p(N, P)$ and the per capita impact of the predator $G_p(N, P)$ are not coupled between them. To this aim we prove the following:

Proposition: There exists a parameter $p_0 \in (]0; +\infty[)^6$ *such that, for any* $(N; P) \in (]0; +\infty[)^2$:

z (*i*) *there exists* $x_0 \in E$, *only depending on* p_0, *that verifies* $\Omega(x_0) = 0$
(*ii*) g_{p_0} *and* H_{p_0} *are not proportional to each other*;
(*iii*) g_{p_0} *and* G_{p_0} *are not proportional to each other*;
(*iv*) H_{p_0} *and* G_{p_0} *are not proportional to each other*;
(*v*) *the solutions of the aggregated system are bounded*.

The meaning of these claims is:

(1) there exists an equilibrium (u_1^*, v_1^*) of the fast part of the dynamics with all the migration parameters having positive values;
(2) there exists a parameter vector such that the per capita predator impact, the numerical response and the functional response are not proportional to each other,
(3) the solutions of the aggregated model are bounded, and hence, according to the Centre Manifold Theorem, the dynamics of the aggregated system approximates that of the full system without time limitation.

Proof of the proposition: We use the Implicit Function Theorem (Cartan, 1966) in order to prove (i). Let $(N; P)$ be a fixed positive parameter. Remark that if $p = p^* = (\alpha^*; \beta^*; \gamma^*; \delta^*; 0; 0)$ where all non-zero components are positive, then (C.1) gives the migration rates of our example 1. In this case the solution of (C.3) is $x^* = (u_1^*; v_1^*; p^*)$ with

$$u_1^* = \frac{2\alpha^*}{\alpha^* + \sqrt{(\alpha^*)^2 + 4\alpha^*\beta^* N}}; \quad v_1^* = \frac{\gamma^* u_1^* N}{\delta^* + \gamma^* u_1^* N}. \tag{C.4}$$

Note that both u_1^* and v_1^* are in $]0; 1[$ for each $(N; P) \in (]0; +\infty[)^2$. Furthermore, if we denote $\Omega = (\Omega_1; \Omega_2)$, then

$$\left| \frac{D\Omega}{D(u_1; v_1)}(x^*) \right| = \begin{vmatrix} \frac{\partial \Omega_1}{\partial u_1}(x^*) & \frac{\partial \Omega_1}{\partial v_1}(x^*) \\ \frac{\partial \Omega_2}{\partial u_1}(x^*) & \frac{\partial \Omega_2}{\partial v_1}(x^*) \end{vmatrix}$$

$$= (\alpha^* + 2\beta^* u_1^* N)\left(\gamma^* + \frac{\delta}{u_1^* N}\right) > 0, \tag{C.5}$$

and hence, by the Implicit Function Theorem, there exist an open neighbourhood U_1 of $(u_1^*; v_1^*)$ in $(]0; 1[)^2$, an open neighbourhood U_2 of p^* in R^6, and a map $\varphi: U_2 \to U_1$, such that:

$$\forall x \in U_1 \times U_2, \Omega(x) = 0 \Leftrightarrow (u_1; v_1) = \varphi(p). \tag{C.6}$$

Note that the linearisation of the fast part of the dynamics [r.h.s. of (5)] of example 3 around the equilibrium is a perturbation of the linearisation of the fast dynamics of example 1, which has a hyperbolically stable equilibrium. Thus in example 3, the equilibrium $\varphi(p)$ obtained by the Implicit Function Theorem is also hyperbolically stable. As U_2 is an open set containing p^*, which is on the bound of $(]0; +\infty[)^6$, if follows that $U_2 \cap (]0; +\infty[)^6$ is a non-empty open set. Hence, by considering p in this set and by putting $x_0 = (\varphi(p); p)$, (i) follows.

In order to prove (ii), we recall that the Implicit Function Theorem claims that if Ω is of class C^1 then φ is also of class C^1. Moreover, it follows from (7–12) that the predator ration, the numerical response and the per capita impact of the predator are C^1 with respect to the equilibrium frequencies. Therefore g_p, H_p, and G_p are C^1 with respect to p. Here we can write:

$$g_p(N, P) = g_{p^*}(N, P) + O(\|p - p^*\|), \tag{C.7a}$$

$$H_p(N, P) = H_{p^*}(N, P) + O(\|p - p^*\|). \tag{C.7b}$$

Then, by using (C.7) and the Taylor expansion, we obtain:

$$\frac{g_p(N; P)}{H_p(N; P)} = \frac{g_{p^*}(N; P)}{H_{p^*}(N; P)} + O(\|p - p^*\|). \tag{C.8}$$

We have seen in example 1 that the l.h.s. of (C.8) actually depends on N, hence if the parameter p is sufficiently close to p^*, the r.h.s. of (C.8) also depends on N. This proves (ii).

In fact, we have demonstrated the existence of a parameter p for which the predator ration and the numerical response are not proportional to each other. Note that this result does not depend on the value of $\delta \in]0; +\infty[$. Let $\tilde{p} = (\alpha^*; \beta^*; \gamma^*; 0; \lambda^*; \sigma^*)$ be the value of p from example 2. Similar arguments to those above prove that

$$\frac{g_p(N; P)}{G_p(N; P)} = \frac{g_{\tilde{p}}(N; P)}{G_{\tilde{p}}(N; P)} + O(\|p - \tilde{p}\|). \tag{C.9}$$

In consequence, if p is sufficiently close to $\tilde{p}$, then the per capita impact of the predator is not proportional to the predator ration. In order to prove the proposition, we need to exhibit a parameter p such that (ii) and (iii) are simultaneously satisfied. If the parameters δ, λ and σ are small enough, then p^* and $\tilde{p}$ are arbitrary close. Hence there exists p_0 such that $O(\|p_0 - \tilde{p}\|)$ and $O(\|p_0 - p^*\|)$ are both close enough to zero and then (iii) follows.

Once again, similar arguments to those used above lead us to write:

$$\frac{G_p(N; P)}{H_p(N; P)} = \frac{G_{p^*}(N; P)}{H_{p^*}(N; P)} + O(\|p - p^*\|). \tag{C.10}$$

As this ratio is not a constant when $p = p^*$, then it is

not a constant when $p = p_0$ because p_0 may be arbitrary close to p^*. We conclude that if p equals p_0, then H_{p_0} and G_{p_0} are not proportional to each other. This ends the proof of (iv).

To prove (v) note that in the absence of predators, the prey growth is logistic [described by (17)] and thus prey density is bounded. As prey can only suffer from the presence of predators, their density remains always bounded. As the predator density is limited by their food (i.e., prey), the predator density is bounded as well.