Pergamon

Mathl. Comput. Modelling Vol. 27, No. 4, pp. 51–61, 1998

0895-7177/98 $19.00 + 0.00

PII: S0895-7177(98)00005-3

Lotka-Volterra's Model and Migrations: Breaking of the Well-Known Center

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Abstract—This paper is devoted to the study of the effect of individual behavior on the Lotka-Volterra predation. We assume that the individuals have many activities in a day for example. Each population is subdivided into subpopulations corresponding to different activities. In order to be clear, I have chosen the case of two activities for each population. We assume that the activities change is faster than the other processes (reproduction, mortality, predation...). This means that we consider population in which the individuals change their activities many times in a day while the reproduction and the predation effects are sensible after about ten days, for example. We use the aggregation method developed in [1] to obtain the global dynamics. Indeed, we start with a micro-model governing the micro-variables, which are the subpopulation densities; the aggregation method permits us to obtain a simpler system governing the macro-variables, which are the global population densities. Furthermore, this method allows us to observe emergence of the dynamics. Indeed, the method implies that the dynamics of the micro-system is close to an invariant manifold after a short time. We show that the dynamics on this manifoid is a perturbation of the well-known center of the Lotka-Volterra model. Finally, we prove that a weak change of behavior can lead to a subcritical Hopf bifurcation in the global dynamics.

Keywords—Predator-prey models, Migrations, Perturbations, Center manifold, Bifurcation.

INTRODUCTION

Predation plays a crucial role in population dynamics because it determines the biomass transferred in the biocoenosis. Among all the existing predation models, the simplest is the Lotka-Volterra's model which is based on three assumptions:

- the Malthus Law is applied for both populations, that is the prey has an exponential growth in the absence of predators and the predator has an exponential decay in the absence of prey;
- the Mass Action Law is applied for the predation, that is the number of prey disappearing per unit time is proportional to the number of encounters;
- the predator density growth is proportional to the density of eaten prey.

Many authors have shown various paradoxes implied by this model and they proposed more realistic models. The first objection of the Lotka-Volterra model is that every solution is periodic: it presents a center. In our paper, we consider this model together with a behavioral dynamics. We consider two activities for each population and fast changes. The activities changes are assumed to be constant. We have thus a differential system with four equations governing each population density in each activity. The aggregation method permits us to reduce the dimension from four to two equations, governing the total population densities. This method is based on a Center Manifold Theorem. The reduced system is in fact the restriction of the initial micro-system to the center manifold. One obtains a macro-system which is a perturbation of the dynamics occurring

Typeset by $\mathcal{A}\mathcal{M}\mathcal{S}$-TEX on each patch, that is the center. As a consequence, we must calculate the perturbation term in order to determine the actual dynamics. We study the macro-system and we show that even a weak change in the behavioral parameter can have a strong consequence on the global dynamics. In fact, we cause emergence of a Hopf bifurcation by acting on the predator behavior.

In the first section, we apply the reduction method on the micro-model and we exhibit the macro-model with perturbation terms. In the second section, we choose an example where the macro-model is completely determined. We show that the dynamics presents a stable or unstable focus, according to the parameters values. Furthermore, we prove in the third section that when the parameters associated to the predator migration are modified (even weakly), a subcritical bifurcation occurs at the population level.

MICRO-MODEL AND MACRO-MODEL

This section is devoted to the description and the first treatment of our micro-model. Let n_i^α be the density of population α on patch i ($i \in \{1,2\}$ and $\alpha \in \{1,2\}$). Population 1 is the prey population and population 2 is the predator population. Our model is the following:

$$\begin{aligned}
\frac{dn_1^1}{dt} &= R\left(k_{12}^1 n_2^1 - k_{21}^1 n_1^1\right) + n_1^1\left(a^1 - b_{11}^{12} n_1^2 - b_{12}^{12} n_2^2\right),\\
\frac{dn_2^1}{dt} &= R\left(k_{21}^1 n_1^1 - k_{12}^1 n_2^1\right) + n_2^1\left(a^1 - b_{21}^{12} n_1^2 - b_{22}^{12} n_2^2\right),\\
\frac{dn_1^2}{dt} &= R\left(k_{12}^2 n_2^2 - k_{21}^2 n_1^2\right) - n_1^2\left(a^2 - b_{11}^{21} n_1^1 - b_{12}^{21} n_2^1\right),\\
\frac{dn_2^2}{dt} &= R\left(k_{21}^2 n_1^2 - k_{12}^2 n_2^2\right) - n_2^2\left(a^2 - b_{21}^{21} n_1^1 - b_{22}^{21} n_2^1\right).
\end{aligned} \tag{1}$$

The coefficient a^α is the growth rate of population α. For the sake of simplicity, we assume that it does not depend on the activity. The coefficient b_{ij}^{12} is the rate of prey in activity i eaten by a predator in activity j. b_{ij}^{21} is the growth rate of predator in activity i due to predation on prey in activity j. $R \gg 1$ is the time scale factor: it means that the change of activities is faster than the other processes. The parameter k_{ij}^α is the rate of population α switching from activity j to activity i. It is assumed to be a constant.

Let $n^\alpha = n_1^\alpha + n_2^\alpha$ be the total densities. Let $u_i = n_i^1/n^1$ the prey frequency in activity i and let $v_i = n_i^2/n^2$ the predator frequency in activity i. We can write system (1) as

$$\begin{aligned}
\frac{du_i^1}{d\tau} &= k_{12}^1 u_2^1 - k_{21}^1 u_1^1 + \varepsilon u_1^1\left(\sum_{i=1}^{2}\sum_{j=1}^{2} b_{ij}^{12} u_i^1 u_j^2 - \left(b_{11}^{12} u_1^2 + b_{12}^{12} u_2^2\right)\right) n^2,\\
\frac{du_i^2}{d\tau} &= k_{12}^2 u_2^2 - k_{21}^2 u_1^2 + \varepsilon u_1^2\left(\sum_{i=1}^{2}\sum_{j=1}^{2} b_{ij}^{21} u_i^2 u_j^1 - \left(b_{11}^{21} u_1^1 + b_{12}^{21} u_2^1\right)\right) n^1,\\
\frac{dn^1}{d\tau} &= \varepsilon n^1\left(a^1 - \left(\sum_{i=1}^{2}\sum_{j=1}^{2} b_{ij}^{12} u_i^1 u_j^2\right) n^2\right),\\
\frac{dn^2}{d\tau} &= -\varepsilon n^2\left(a^2 - \left(\sum_{i=1}^{2}\sum_{j=1}^{2} b_{ij}^{21} u_i^2 u_j^1\right) n^1\right),
\end{aligned} \tag{2}$$

where $\varepsilon = 1/R \ll 1$ and $t \in \varepsilon\tau$.

In this case, the fast dynamics, obtained by putting $\varepsilon = 0$ in (2), has a hyperbolically stable equilibrium. It is the solution of the linear system

$$\begin{aligned} k_{12}^1 u_2^1 - k_{21}^1 u_1^1 &= 0, \qquad u_2^1 = 1 - u_1^1, \\ k_{12}^2 u_2^2 - k_{21}^2 u_1^2 &= 0, \qquad u_2^2 = 1 - u_1^2. \end{aligned} \tag{3}$$

It follows that the solutions are

$$\begin{aligned} U_1^\alpha &= \frac{k_{12}^\alpha}{k_{12}^\alpha + k_{21}^\alpha}, \\ U_2^\alpha &= \frac{k_{21}^\alpha}{k_{12}^\alpha + k_{21}^\alpha}, \end{aligned} \tag{4}$$

and a simple calculation shows that the eigenvalues of the Jacobian matrix associated to the fast part, at the equilibrium given by (4), are $-(k_{12}^\alpha + k_{21}^\alpha)$. They are strictly negative. Now, the reduction method can be applied.

We consider the relative frequencies $\bar{u}_i^\alpha = u_i^\alpha - U_i^\alpha$ and then the equilibrium frequencies are now at zero. Our model (2) can now be written as follows:

$$\begin{aligned} \frac{d\bar{u}_i^1}{d\tau} &= k_{12}^1 \bar{u}_2^1 - k_{21}^1 \bar{u}_1^1 \\ &\quad + \varepsilon \left(\bar{u}_1^1 + U_1^1\right) \cdot \left(\sum_{i=1}^{2} \sum_{j=1}^{2} b_{ij}^{12} \left(\bar{u}_i^1 + U_i^1\right)\left(\bar{u}_j^2 + U_j^2\right) - \sum_{j=1}^{2} b_{1j}^{12} \left(\bar{u}_j^2 + U_j^2\right) \right) n^2, \\ \frac{d\bar{u}_i^2}{d\tau} &= k_{12}^2 \bar{u}_2^2 - k_{21}^2 \bar{u}_1^2 \\ &\quad - \varepsilon \left(\bar{u}_1^2 + U_1^2\right) \cdot \left(\sum_{i=1}^{2} \sum_{j=1}^{2} b_{ij}^{21} \left(\bar{u}_i^2 + U_i^2\right)\left(\bar{u}_j^1 + U_j^1\right) - \sum_{i=1}^{2} b_{1i}^{21} \left(\bar{u}_i^1 + U_i^1\right) \right) n^1, \\ \frac{dn^1}{d\tau} &= \varepsilon n^1 \left(a^1 - \left(\sum_{i=1}^{2} \sum_{j=1}^{2} b_{ij}^{12} \left(\bar{u}_i^1 + U_i^1\right)\left(\bar{u}_j^2 + U_j^2\right) \right) n^2 \right), \\ \frac{dn^2}{d\tau} &= -\varepsilon n^2 \left(a^2 - \left(\sum_{i=1}^{2} \sum_{j=1}^{2} b_{ij}^{21} \left(\bar{u}_i^2 + U_i^2\right)\left(\bar{u}_j^1 + U_j^1\right) \right) n^1 \right). \end{aligned} \tag{5}$$

Let

$$\begin{aligned} b^1 &= \sum_{i=1}^{2} \sum_{j=1}^{2} b_{ij}^{12} U_i^1 U_j^2, \\ b^2 &= \sum_{i=1}^{2} \sum_{j=1}^{2} b_{ij}^{21} U_i^2 U_j^2. \end{aligned}$$

The Global Center Manifold Theorem (see [1–4]) states that the global dynamics is in a short time close to the solutions of the following macro-model:

$$\begin{aligned} \frac{dn^1}{dt} &= n^1 \left(a^1 - b^1 n^2\right) + n^1 O(\varepsilon), \\ \frac{dn^2}{dt} &= -n^2 \left(a^2 - b^2 n^1\right) + n^2 O(\varepsilon). \end{aligned} \tag{6}$$

As the parameters k_{ij}^α are assumed to be constant, the equilibrium frequencies are constant. We conclude that if ε is null, the model (6) is the Lotka-Volterra model. This model presents a center in the positive orthant which is not a structurally stable dynamics. Hence, the perturbation term cannot be neglected. In order to determine the actual global dynamics, it is necessary to calculate at least the next term in the asymptotic expansion with respect to ε.

ASYMPTOTIC EXAPANSION AND STUDY ON THE CENTER MANIFOLD

First Term in the Expansion

The method used for calculating the following terms in the asymptotic expansion can be found for example in [1]. On the center manifold, we have: $\bar{u}_i^\alpha = \varepsilon\omega_{i1}^\alpha(n^1, n^2) + O(\varepsilon)$, for every (n^1, n^2) in a given closed and bounded set Δ in the plane. We replace u_i^α by its expression in the equations of system (5) and obtain

$$\begin{aligned} \frac{d\bar{u}_1^1}{d\tau} &= \varepsilon\left(k_{12}^1\omega_{21}^1 - k_{21}^1\omega_{11}^1 + U_1^1\left[b^1 - \left(b_{11}^{12}U_1^2 + b_{12}^{12}U_2^2\right)\right]n^2\right) + O\left(\varepsilon^2\right), \\ \frac{d\bar{u}_1^2}{d\tau} &= \varepsilon\left(k_{12}^2\omega_{21}^2 - k_{21}^2\omega_{11}^2 - U_1^2\left[b^2 - \left(b_{11}^{21}U_1^1 + b_{12}^{21}U_2^1\right)\right]n^1\right) + O\left(\varepsilon^2\right). \end{aligned} \tag{7}$$

Furthermore, we can write

$$\frac{d\bar{u}_i^\alpha}{d\tau} = \frac{\partial\bar{u}_i^\alpha}{\partial n^1}\frac{dn^1}{d\tau} + \frac{\partial\bar{u}_i^\alpha}{\partial n^2}\frac{dn^2}{d\tau} = O\left(\varepsilon^2\right).$$

As a consequence, by using $\omega_{21}^\alpha = -\omega_{11}^\alpha$, we can conclude

$$\begin{aligned} \omega_{11}^1 &= \frac{U_1^1\left(b^1 - \left(b_{11}^{12}U_1^2 + b_{12}^{12}U_2^2\right)\right)}{k_{12}^1 + k_{21}^1}n^2, \\ \omega_{11}^2 &= -\frac{U_1^2(b^2 - (b_{11}^{21}U_1^1 + b_{12}^{21}U_2^1))}{k_{12}^2 + k_{21}^2}n^1. \end{aligned} \tag{8}$$

Finally, we replace ω_{i1}^α by its expression in the last two equations of system (5) and deduce the following system (9):

$$\begin{aligned} \frac{dn^1}{dt} &= n^1\left[a^1 - n^2\left(b^1 + \varepsilon\left(c^{11}n^1 + c^{12}n^2\right)\right)\right] + O\left(\varepsilon^2\right), \\ \frac{dn^2}{dt} &= -n^2\left[a^2 - n^1\left(b^2 + \varepsilon\left(c^{21}n^1 + c^{22}n^2\right)\right)\right] + O\left(\varepsilon^2\right), \end{aligned} \tag{9}$$

where

$$\begin{aligned} c^{11} &= -\frac{U_1^2\left(b^2 - \left(b_{11}^{21}U_1^1 + b_{12}^{21}U_2^1\right)\right)}{k_{12}^2 + k_{21}^2}\left[\left(b_{11}^{12} - b_{12}^{12}\right)U_1^1 + \left(b_{21}^{12} - b_{22}^{12}\right)U_2^1\right], \\ c^{12} &= \frac{U_1^1\left(b^1 - \left(b_{11}^{12}U_1^2 + b_{12}^{12}U_2^2\right)\right)}{k_{12}^1 + k_{21}^1}\left[\left(b_{11}^{12} - b_{21}^{12}\right)U_1^2 + \left(b_{12}^{12} - b_{22}^{12}\right)U_2^2\right], \\ c^{21} &= -\frac{U_1^2\left(b^2 - \left(b_{11}^{21}U_1^1 + b_{12}^{21}U_2^1\right)\right)}{k_{12}^2 + k_{21}^2}\left[\left(b_{11}^{21} - b_{21}^{21}\right)U_1^1 + \left(b_{12}^{21} - b_{22}^{21}\right)U_2^1\right], \\ c^{22} &= \frac{U_1^1\left(b^1 - \left(b_{11}^{12}U_1^2 + b_{12}^{12}U_2^2\right)\right)}{k_{12}^1 + k_{21}^1}\left[\left(b_{11}^{21} - b_{12}^{21}\right)U_1^2 + \left(b_{21}^{21} - b_{22}^{21}\right)U_2^2\right]. \end{aligned} \tag{10}$$

Local Study of the Dynamics

We study in this section, the vector field X_ε defined by (9), on a compact set in the positive orthant, in the generic case, that is for an open and dense set Λ in the space of parameters. We shall study in the next section an example where the parameters cross transversally the complementary set of Λ.

When ε is null in (9), the vector field associated X_0 has a nondegenerate center in the positive orthant. Let Δ be a compact set in the positive orthant. For a sufficiently small value of ε, the vector field X_ε has only one singularity in Δ. This singularity is close to that of X_0. Let us study this singularity. As we are in the positive orthant, which has boundary invariant under the flow of X_ε, the function $f : (n^1, n^2) \mapsto 1/n^1 n^2$ is well defined and positive. As a consequence, the vector field $\tilde{X}_\varepsilon = f \cdot X_\varepsilon$ has the same orbits as X_ε. Now, we study $\tilde{X}_\varepsilon$. When ε is null, this vector field is an Hamiltonian vector field, that is there exists a function H such that the vector field can be written as follows:

$$\frac{dn^1}{dt} = -\frac{\partial H}{\partial n^2}\left(n^1, n^2\right),$$
$$\frac{dn^2}{dt} = \frac{\partial H}{\partial n^1}\left(n^1, n^2\right).$$

In the following, we denote by $\dot{x}$ the derivative of x with respect to the time t. The expression of $\tilde{X}_\varepsilon$ is

$$\begin{aligned}
\dot{n}^1 &= \frac{a^1}{n^2} - \left(b^1 + \varepsilon\left(c^{11}n^1 + c^{12}n^2\right)\right) + O\left(\varepsilon^2\right) \\
&= -\frac{\partial H}{\partial n^2}\left(n^1, n^2\right) + O(\varepsilon^2), \\
\dot{n}^2 &= -\frac{a^2}{n^1} + \left(b^2 + \varepsilon\left(c^{21}n^1 + c^{22}n^2\right)\right) + O\left(\varepsilon^2\right) \\
&= \frac{\partial H}{\partial n^1}\left(n^1, n^2\right) + O(\varepsilon^2),
\end{aligned} \tag{11}$$

where $H(n^1, n^2) = b^1 n^2 - a^1 \ln(n^2) + b^2 n^1 - a^2 \ln(n^1) + C$. The constant can be chosen such that H is null at the singularity of the nonperturbated vector field. Let $(\bar{n}^1, \bar{n}^2)$ be the coordinates of the singularity of $\tilde{X}_0$. A straightforward computation permits the verification of

$$\bar{n}^1 = \frac{a^2}{b^2} \quad \text{and} \quad \bar{n}^2 = \frac{a^1}{b^1}.$$

Let $(\bar{n}^1_\varepsilon, \bar{n}^2_\varepsilon)$ be the coordinates of the singularity C_ε of $\tilde{X}_\varepsilon$. The Implicit Function Theorem allows us to conclude that these coordinates are at least C^1 with respect to ε. By using the Taylor Theorem, we have

$$\bar{n}^1_\varepsilon = \bar{n}^1 + O(\varepsilon),$$
$$\bar{n}^2_\varepsilon = \bar{n}^2 + O(\varepsilon).$$

Let $D\tilde{X}_\varepsilon(C_\varepsilon)$ be the linear part of $\tilde{X}_\varepsilon$ at C_ε. It is given by

$$\begin{aligned}
\dot{n}^1 &= -\varepsilon c^{11} n^1 - \left(\frac{a^1}{(\bar{n}^2)^2} + O(\varepsilon)\right) n^2 + O\left(\varepsilon^2\right), \\
\dot{n}^2 &= -\left(\frac{a^2}{(\bar{n}^1)^2} + O(\varepsilon)\right) n^1 + \varepsilon c^{22} n^2 + O\left(\varepsilon^2\right).
\end{aligned} \tag{12}$$

We conclude that if ε is sufficiently small, C_ε is either a stable focus, an unstable focus, or a center. In fact, if the trace of the linear part is positive, the focus is unstable. If the trace is negative, the focus is stable. If this trace is null, we can conclude that the singularity is a center for the linear part, but we cannot conclude this for the whole vector field $\tilde{X}_\varepsilon$.

Let $\operatorname{Tr}(\tilde{X}_\varepsilon)$ be the trace of the linear part. It can be expressed as follows:

$$\operatorname{Tr}\left(\tilde{X}_\varepsilon\right) = d_1 \cdot \varepsilon + O\left(\varepsilon^2\right),$$

where $d_1 = (-c^{11}+c^{22})$. Furthermore, the coefficients c^{ij} are functions depending on the parameters of system (2). In particular, they depend on the activities-changes, that is on the behavior. There are three cases:

(i) $d_1 > 0$: in this case, for ε sufficiently small, C_ε is an unstable focus;
(ii) $d_1 < 0$: in this case, for ε sufficiently small, C_ε is a stable focus;
(iii) $d_1 = 0$: in this case, we cannot conclude anything *a priori*.

The coefficient d_1 is an analytic function with respect to the parameters. If follows that the set $\{d_1 = 0\}$ in the parameters space has an open dense complementary set. In other words, if Λ is the set $\{d_1 \neq 0\}$ then it is an open dense set in the parameters space. For every parameter vector in Λ, we can give the nature of the singularity of $\tilde{X}_\varepsilon$, if ε is sufficiently small.

This ends the local study near the singularity, when the parameter vector is in Λ. Let us now study the global dynamics (limit cycles, etc...).

Global Study of the Dynamics

In this section, we use some techniques of the Perturbation theory which can be found for example in [5–7]. Let us consider ω_ε, the dual form of the vector-field $\tilde{X}_\varepsilon$. From (11), we know that

$$\omega_\varepsilon\left(n^1,n^2\right) = dH\left(n^1,n^2\right) + \varepsilon\eta\left(n^1,n^2\right) + o(\varepsilon), \tag{13}$$

where

$$\eta\left(n^1,n^2\right) = \left(c^{21}n^1 + c^{22}n^2\right) dn^1 + \left(c^{11}n^1 + c^{12}n^2\right) dn^2.$$

The function H is defined just after (11). It is a Morse function. Let Σ be a section transversal with respect to the curves $\{H = C^{te}\}$ and $0 \in \Sigma$. We can define the Poincaré map P_ε on Σ. With these notations, the limit cycles are given by the roots of the *moving map* δ_ε, defined as $h \mapsto \delta_\varepsilon = P_\varepsilon(h) - h$. The Poincaré lemma allows us to write

$$\delta(h,\varepsilon) = -\varepsilon \int_{\{H=h\}} \eta + o(\varepsilon).$$

Let $I_1(h)$ be the first coefficient in the expansion of $\delta(h,\varepsilon)$ with respect to ε. The sign of I_1 gives the sign of δ for ε sufficiently small. We determine the sign of I_1.

$$\begin{aligned} I_1(h) &= -\int_{\{H=h\}} \left(c^{21}n^1 + c^{22}n^2\right) dn^1 + \left(c^{11}n^1 + \left(c^{12}n^2\right) n^2\right) dn^2 \\ &= -\iint_{\{H\le h\}} \left(c^{11} - c^{22}\right) dn^1 \wedge dn^2 \\ &= d_1 \iint_{\{H\le h\}} dn^1 \wedge dn^2. \end{aligned}$$

The second equality above is an application of the Stockes Theorem. Let

$$A(h) = \iint_{\{H\le h\}} dn^1 \wedge dn^2.$$

$A(h)$ is the area of the topological disc $\{H \le h\}$ and it is then a strictly positive real number for every h values. Consequently, the sign of I_1 is the same as that of d_1 and thus, it does not depend on h. We conclude that for $d_1 > 0$, the solutions of the model are unbounded: they leave every neighborhood of the singularity (if ε is small enough). If $d_1 < 0$, the solutions converge to the singularity. Finally, if $d_1 = 0$, we can not conclude anything *a priori*.

Now, assume that we can make a parameter vary. We suppose that for the initial parameter value, $d_1 < 0$ and for the final parameter value, $d_1 > 0$, all that for a fixed ε value. Between its initial and final value, the parameter crosses a bifurcation value. We analyse this case in the following section.

BIFURCATION ON THE CENTER MANIFOLD

Mathematical Study

In this section, we exhibit a Hopf bifurcation on the center manifold. Furthermore, we show that this bifurcation is generic and that it is a subcritical Hopf bifurcation. In order to show this, we consider a one parameter subfamily of the family defined by system (1). Then we vary the parameter of this subfamily. When this parameter increases, we show that the singularity in the positive orthant switches from a stable to an unstable one. Simultaneously, a stable limit cycle appears around the singularity. In other words, at the beginning, the solutions converge to the singularity and after the bifurcation, they oscillate around the same singularity.

In a first step, we show that the trace of the vector field linear part, depending on the parameter, near the singularity, changes its sign. In the second step, we point out the birth of the stable limit cycle around the singularity by proving that the third derivative of the moving map is not null at the bifurcation parameter value.

We choose the following one parameter subfamily:

$$\begin{aligned}
\frac{dn_1^1}{d\tau} &= \left[n_2^1 - 2n_1^1\right] + \varepsilon n_1^1\left[2 - 2.93n_1^2 - 0.2n_2^2\right],\\
\frac{dn_2^1}{d\tau} &= \left[2n_1^1 - n_2^1\right] + \varepsilon n_2^1\left[2 - n_1^2 - 0.5n_2^2\right],\\
\frac{dn_1^2}{d\tau} &= \left[(1+\lambda)n_2^2 - 3n_1^2\right] - \varepsilon n_1^2\left[3 - 0.59n_1^1 - 0.2n_2^1\right],\\
\frac{dn_2^2}{d\tau} &= \left[3n_1^2 - (1+\lambda)n_2^2\right] - \varepsilon n_2^2\left[3 - n_1^1 - 0.3n_2^1\right].
\end{aligned} \tag{14}$$

It is a model like (1). We can thus reduce it into a model like (9). The parameter λ is free: it can take values between -1 and $+\infty$. When we change this parameter value, we obtain a bifurcation of the global dynamics. A straightforward calculation shows that the parameters of the reduced system (on the center manifold) are

$$a^1 = 2, \qquad a^2 = 3, \qquad b^1 = \frac{145.05 + 83.85\lambda}{51(4+\lambda)}, \qquad b^2 = \frac{98.4 + 16.8\lambda}{51(4+\lambda)}.$$

We know from the previous section, that the first coefficient $d_1(\lambda)$ in the expansion of the trace of the vector field, on the center manifold, with respect to the parameter ε, is given by the coefficients c^{11} and c^{22}. These coefficients can be calculated with formulae (10). We obtain

$$\begin{aligned}
c^{11}(\lambda) &= -\frac{659.88(1+\lambda)}{867(4+\lambda)^3},\\
c^{22}(\lambda) &= -\frac{659.88 + 1503.09\lambda + 527.25\lambda^2 + 46.18\lambda^3}{867(4+\lambda)^3}.
\end{aligned}$$

We deduce the $d_1(\lambda)$

$$d_1(\lambda) = \lambda \cdot \frac{1503.09 + 527.25\lambda + 48.18\lambda^2}{867(4+\lambda)^3}.$$

As a consequence, $d_1(0) = 0$. Briefly, the behavior of $d_1(\lambda)$ for λ close to 0 is given by

$$\left.\frac{d(d_1(\lambda))}{d\lambda}\right|_{\lambda=0} = d_1^1 = \frac{1503.09}{3468} > 0.$$

We conclude that if λ is close to 0 and has a negative value, then $d_1(\lambda) < 0$ and if λ is close to 0 and has a positive value, then $d_1(\lambda) > 0$.

Let $\mathrm{Tr}\,(\lambda, \varepsilon)$ be the trace of the linear part of the vector-field on the center manifold, at the singularity in the positive orthant. If the sign of this trace changes when the parameter λ increases, then the singularity, initially stable, becomes unstable: there is a Hopf bifurcation. We show that this bifurcation occurs for a small enough fixed ε value. In fact, it is a consequence of the Implicit Function Theorem. Indeed, we have

$$\mathrm{Tr}\,(\lambda, \varepsilon) = \varepsilon \cdot (d_1(\lambda) + O(\varepsilon)).$$

Therefore, the sign of $\mathrm{Tr}\,(\lambda, \varepsilon)$ is the same as the sign of $\tilde{\mathrm{Tr}}\,(\lambda, \varepsilon)$ where

$$\tilde{\mathrm{Tr}}\,(\lambda, \varepsilon) = d_1(\lambda) + O(\varepsilon).$$

We have seen that

$$\tilde{\mathrm{Tr}}\,(0,0) = 0,$$
$$\frac{\partial \tilde{\mathrm{Tr}}}{\partial \lambda}(0,0) = \left.\frac{d(d_1(\lambda))}{d\lambda}\right|_{\lambda=0} \neq 0.$$

The Implicit Function Theorem permits the conclusion that in a (0,0) neighborhood, in the parameter space $\{(\lambda, \varepsilon)\}$, the function $\tilde{\mathrm{Tr}}$ vanishes on a curve, which is the graph of a function $\varepsilon \mapsto \lambda(\varepsilon)$. The conclusion is also valid for the function Tr, if ε is not null.

If $\varepsilon_0 \neq 0$ is fixed in a neighborhood of zero, there is a unique value of the parameter λ, such that $\mathrm{Tr}\,(\varepsilon_0, \lambda_0)$ vanishes. It means that when λ crosses the λ_0 value, then a Hopf bifurcation occurs.

From an ecological viewpoint, it means that if $\lambda < \lambda_0$, both populations densities reach an equilibrium. If λ increases and crosses the value λ_0, then this equilibrium becomes unstable: the populations densities oscillates around the unstable equilibrium. It is important to know if these oscillations amplitude increases with time or if they are bounded. We shall see now how these amplitudes depend on λ when this parameter is close to λ_0 (so called *bifurcation value*).

In order to solve this problem, we consider again the moving function $\delta(h, \lambda, \varepsilon)$. When this function vanishes, it implies the existence of limit cycle. The solutions of the model contained in the compact set bounded by this limit cycle are bounded. Let us summarize the results in the following way. Fix ε and λ in a (0,0)-neighborhood. We can distinguish four cases:

(i) if $\delta(h, \lambda, \varepsilon) > 0$, the oscillations amplitude increases;
(ii) if $\delta(h, \lambda, \varepsilon) < 0$, the oscillations amplitude decreases;
(iii) if $\delta(h, \lambda, \varepsilon) \equiv 0$, all trajectories are periodic: the oscillation amplitude is constant;
(iv) if $\delta(h, \lambda, \varepsilon) = 0$ for a given value h_0 of h, the trajectory γ_{h_0} passing through h_0 is periodic, and the trajectories passing through $h < h_0$ oscillate with a amplitude bounded by that of γ_{h_0}.

Let us consider the function δ associated to the vector field obtained in the center manifold. As we have seen, when the function δ is close to zero, the first coefficient $I_1(h, \lambda)$, in the expansion with respect to the powers of ε, is close to zero. Thus, it could be smaller than the other terms of the expansion. We make a change of parameter to avoid this problem.

As ε is fixed to a positive value ε_0 close to zero, let $\lambda = \mu\varepsilon$ and let $\mu_0 = \lambda_0/\varepsilon_0$. With these notations, the dual-form of the vector field on the center manifold, after multiplying by the positive function $(n^1, n^2) \mapsto 1/n^1 n^2$ is

$$\omega_\varepsilon = dH + \varepsilon\eta_1 + \varepsilon^2\eta_2 + o\left(\varepsilon^2\right).$$

As we have seen

$$
\begin{aligned}
\eta_1 &= \left(c^{21}n^1 + c^{22}n^2\right) dn^1 + \left(c^{11}n^1 + c^{12}n^2\right) dn^2 \\
&= d\left[\frac{c^{21}\left(n^1\right)^2 + c^{12}\left(n^2\right)^2}{2}\right] + c^{22}n^2\,dn^1 + c^{11}n^1\,dn^2 \\
&= d\left[\frac{c^{21}\left(n^1\right)^2 + c^{12}\left(n^2\right)^2}{2}\right] + c^{22}\left(n^2\,dn^1 + n^1\,dn^2\right) - d_1 n^1\,dn^2 \\
&= d\left[\frac{c^{21}\left(n^1\right)^2 + c^{12}\left(n^2\right)^2}{2} + c^{22}n^1n^2\right] + d_1 n^1\,dn^2.
\end{aligned}
$$

Let $H'(n^1,n^2) = (c^{21}(n^1)^2 + c^{12}(n^2)^2)/2 + c^{22}n^1n^2 + C^{te}$. We choose the constant such that $H'(\bar{n}^1,\bar{n}^2) = 0$ and let

$$
H_\varepsilon\left(n^1,n^2\right) = H\left(n^1,n^2\right) + \varepsilon H'\left(n^1,n^2\right).
$$

We parametrize the transversal section Σ by the values of H_ε. We can thus write the dual-form ω_ε as follows:

$$
\omega_\varepsilon = dH_\varepsilon + \varepsilon\, d_1(\lambda) n^1\,dn^2 + \varepsilon^2 \eta_2 + o\left(\varepsilon^2\right).
$$

We have proved that $d_1(\lambda) = \lambda\, d_1^1 + o(\lambda)$ with $d_1^1 > 0$. As a consequence,

$$
\omega_\varepsilon = dH_\varepsilon + \varepsilon\lambda\, d_1^1 n^1\,dn^2 + \varepsilon o(\lambda) + \varepsilon^2\eta_2 + o\left(\varepsilon^2\right).
$$

By using the change of parameter $\lambda = \mu\varepsilon$, the dual form becomes

$$
\omega_\varepsilon = dH_\varepsilon + \varepsilon^2\mu\, d_1^1 n^1\,dn^2 + \varepsilon^2\eta_2 + o\left(\varepsilon^2\right).
$$

The moving function is thus given by

$$
\begin{aligned}
\delta(h,\lambda,\varepsilon_0) &= -\varepsilon_0^2 \int_{\{H_{\varepsilon_0}=h\}} \left(\mu\, d_1^1 n^1\,dn^2 + \eta_2\right) + o\left(\varepsilon_0^2\right) \\
&= -\varepsilon_0^2 \int_{\{H=h\}} \left(\mu\, d_1^1 n^1\,dn^2 + \eta_2\right) + o\left(\varepsilon_0^2\right).
\end{aligned}
$$

In order to determine η_2, we must compute the coefficients ω_{i2}^α (see [1,7] for more details). The result is

$$
\begin{aligned}
\omega_{12}^1 &= \frac{n^2}{k_{12}^1 + k_{21}^1}\left[U_1^1\left(\sum_{i=1}^2\sum_{j=1}^2 b_{ij}^{12}\left(\omega_{i1}^1 U_j^2 + \omega_{j1}^2 U_i^1\right) - \sum_{j=1}^2 b_{1j}^{12}\omega_{j1}^2\right) + \omega_{11}^1\left(b^1 - \sum_{j=1}^2 b_{1j}^{12} U_j^2\right)\right], \\
\omega_{12}^2 &= -\frac{n^1}{k_{12}^2 + k_{21}^2}\left[U_1^2\left(\sum_{i=1}^2\sum_{j=1}^2 b_{ij}^{21}\left(\omega_{i1}^2 U_j^1 + \omega_{j1}^1 U_i^2\right) - \sum_{j=1}^2 b_{1i}^{21}\omega_{i1}^1\right) + \omega_{11}^2\left(b^2 - \sum_{j=1}^2 b_{1i}^{21} U_i^1\right)\right],
\end{aligned}
\tag{15}
$$

and we have $\omega_{22}^\alpha = -\omega_{12}^\alpha$. The form η_2 can be written with respect to these coefficients as follows:

$$
\begin{aligned}
\eta_2 = &\left[\sum_{i=1}^2\sum_{j=1}^2 b_{ij}^2 1\left(\omega_{j2}^1 U_i^2 + \omega_{j1}^1\omega_{i1}^2 + U_j^1\omega_{i2}^2\right)\right] dn^1 \\
&+ \left[\sum_{i=1}^2\sum_{j=1}^2 b_{ij}^1 2\left(\omega_{i2}^1 U_j^2 + \omega_{i1}^1\omega_{j1}^2 + U_i^1\omega_{j2}^2\right)\right] dn^2.
\end{aligned}
$$

Replacing the parameters by their values, we obtain

$$\begin{aligned}\eta_2\left(n^1,n^2\right) = &\left(a^1_{20}\left(n^1\right)^2 + a^1_{11}n^1n^2 + a^1_{02}\left(n^2\right)^2\right) dn^1\\ &+ \left(a^2_{20}\left(n^1\right)^2 + a^2_{11}n^1n^2 + a^2_{02}\left(n^2\right)^2\right) dn^2.\end{aligned} \tag{16}$$

Therefore, it is a polynomial form. Its coefficients a^{α}_{ij} are real numbers which depend on the parameter λ (or μ, which is the same). We can now give a general expression for the moving function

$$\begin{aligned}\delta(h,\lambda,\varepsilon_0) &= -\varepsilon_0^2 \int_{\{H=h\}} \left(\mu\, d^1_1 n^1\, dn^2 + \eta_2\right) + o\left(\varepsilon_0^2\right)\\ &= -\varepsilon_0^2 \iint_{\{H\le h\}} \left(\mu\, d^1_1\, dn^1 \wedge dn^2 + d\eta_2\right) + o\left(\varepsilon_0^2\right)\\ &= -\varepsilon_0^2 \iint_{\{H\le h\}} \left(\mu\, d^1_1 + \left(2a^2_{20} - a^1_{11}\right) n^1 + \left(a^2_{11} - 2a^1_{02}\right) n^2\right) dn^1 \wedge dn^2 + o\left(\varepsilon_0^2\right).\end{aligned} \tag{17}$$

If ε_0 is small enough, the sign of δ is the same as that of the first coefficient in the expression with respect to powers of ε. Let $I(h,\lambda) = \tilde{I}(h,\mu)$ be this coefficient: we can expand it with respect to h in a neighborhood of 0, that is close to the singularity of the vector field $\tilde{X}_{\varepsilon_0}$.

In a first step, we consider a new coordinates system in which the function H can be written as

$$(x,y) \mapsto x^2 + y^2.$$

With these coordinates, by considering

$$x = \rho\cos(\theta), \qquad y = \rho\sin(\theta),$$

the integration on the domain $\{H \le h\}$ is the integration on the disc of center 0 and of radius $\rho = \sqrt{h}$. We expand the integral, which depends on ρ and μ. In our example, this expansion gives

$$I(\rho,\mu) = c_2(\mu)\rho^2 + c_4(\mu)\rho^4 + o\left(\rho^4\right),$$

with

(i) $c_2(\mu) > 0$ and $c_4(\mu) > 0$ when $\mu < \mu_0$,
(ii) $c_2(\mu) < 0$ and $c_4(\mu) > 0$ when $\mu > \mu_0$,

μ keeps in a neighborhood of μ_0. In the Case (i), the integral is positive for every ρ close to zero. In the Case (ii), the integral vanishes for ρ close to $\rho_0 = \sqrt{-c_2(\mu)/c_4(\mu)}$, which is close to zero if μ is close to μ_0.

The moving function δ is a ε_0-perturbation of the integral I calculated just above. As a consequence, the number of roots of δ is the same as the number of roots of I (for every ρ close to zero), if the derivative of I with respect to ρ at the roots is not null and if ε_0 is small enough (Implicit Function Theorem).

The Hopf bifurcation is therefore generic: when the parameter λ is smaller than its bifurcation value, there is no limit cycle, and the equilibrium is stable. When the parameter becomes greater than the bifurcation value, a limit cycle appears: it is stable while the equilibrium is now unstable.

Ecological Interpretation

The parameter λ appears in the predators migrations rates. When λ increases, the predators proportion decreases in activity 2 and increases in activity 1. Furthermore, the predators in activity 1 have a larger attack rate than the predators in activity 2. It follows that when λ increases, the predation increases.

Therefore, it seems that an increase of predation causes the system to leave its equilibrium and to oscillate.

CONCLUSION

Effects of individuals behavior on the Lotka-Volterra model was investigated. The aggregation method developed in [1] was used in order to obtain the total population dynamics. The aggregated model is in fact the restriction of the global model on a center manifold. In this paper, the aggregated model is a perturbation of the center of Lotka-Volterra. An asymptotic expansion of the aggregated model was computed and the population dynamics which corresponds to this aggregated model was described. We showed with an example that a change in the individual's behavior can lead to a bifurcation in the dynamics at the population level.

We considered an example where the predators had two activities. In the first one the predators had a larger attack rates than in the second one. A Hopf bifurcation occurs when the predators density in the activity 1 increase. Therefore, the predation can be interpreted as a destabilizing factor: when the predation is smaller than a given threshold (before the bifurcation value), the system reaches a stable equilibrium. However, if the predation is larger than the previous threshold, the system leaves the equilibrium and oscillates.

The aggregation method is thus a good tool for reducing the initial model into a simpler one, where analytical results can be obtained. Furthermore, it allows us to understand how new dynamics emerge at the population level.

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