

Chapter 1

Complex Features in Lotka-Volterra Systems with Behavioral Adaptation

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1.1. Introduction

Lotka-Volterra systems have played a fundamental role for mathematical modelling in many branches of theoretical biology and proved to describe, at least qualitatively, the essential features of many phenomena, see for example Murray [Murray 2002]. Furthermore models of that kind have been considered successfully also in quite different and less mathematically formalized context: Goodwin's model of economic growth cycles [Goodwin 1967] and urban dynamics [Dendrinos 1992] are only two of a number of examples. Such systems can certainly be defined as complex ones and in fact the aim of modelling was essentially to clarify mechanisms rather than to provide actual precise simulations and predictions. With regards to complex systems, we recall that one of their main feature, no matter of the specific definition one has in mind, is adaptation, i. e. the ability to adjust.

Lotka-Volterra systems are a large class of models for interaction among species. Depending on such interactions competition, cooperation or predator-prey situations can

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occur, giving rise to further classifications. The dynamics depends on parameters intrinsic to the species, typically growth rate and carrying capacity, and on the coefficients of interaction among the species, which however are often more difficult to specify.

Here we focus on competition among species and, differently from the classical case, we consider for them a kind of “learning skill”: the ability to compete is proportional to the average number of contacts between species in their past, with a weak exponential delay kernel providing a “fade-out” memory effect. Adaptation in such a form is shown to be a mechanism able to establish the appearance of a variety of behaviors, different from equilibria, as distinct kinds of oscillations and chaotic patterns. Furthermore, even for given parameter values, the system can show striking features of multiplicity of attractors. This kind of “complexity” comes out as collective behavior emerging from the interactions among the species involved.

1.2. The model

We consider the general competitive Lotka-Volterra system for n species

$$\frac{dN_i}{dt} = r_i \left[1 - \frac{N_i}{k_i} \right] N_i - \sum_j \alpha_{ij} N_i N_j \quad 1 \leq i, j \leq n, \quad j \neq i, \quad (1)$$

with

$$\alpha_{ij}(t) = \int_{-\infty}^t N_i(u) N_j(u) K_{T_j}(t-u) du \quad 1 \leq i, j \leq n, \quad j \neq i, \quad (2)$$

$N_i(t)$ denotes the density of the i -species at time t , the positive parameters r_i and k_i stand respectively for the intrinsic growth rate and the carrying capacity of i -species. The positive continuous function α_{ij} represents the interaction coefficient between the j and i species. The delay kernel K_T is chosen as in [Noonburg 1986],

$$K_T = \frac{e^{-t/T}}{T}$$

as it provides a reasonable effect of short term memory.

In this case, the set of integro-differential equations (1)-(2) is equivalent to the following set of ordinary differential equations [Lacitignola & Tebaldi 2005],

$$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 (1 - c_1 N_1) - \sum_j \alpha_{1j} N_1 N_j & 1 \leq i, j \leq n, \quad j \neq 1 \\ \frac{dN_i}{dt} = r_i N_i (1 - c_i N_i) - \sum_j \alpha_{ij} N_i N_j & 1 \leq i, j \leq n, \quad j \neq i, \quad i \neq 1 \\ \frac{d\alpha_{ij}}{dt} = \frac{N_i N_j - \alpha_{ij}}{T_j} & 1 \leq i, j \leq n, \quad j \neq i \end{cases} \quad (3)$$

where c_i is the reciprocal of the carrying capacity k_i .

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Having the main aim to discuss the role of the interactions, we consider species with the same adaptation rate T and the same carrying capacity k , except for one.

Such a model can allow to investigate the connectivity problem [May 1973] for competitive Lotka-Volterra systems, strictly related with the role of interactions, also starting to take into account some kind of species differentiation.

The n -species system with $r_i = 1$, $c_i = c$, $T_i = T$, for all $i = 1, \dots, n$ has been extensively investigated [Bortone & Tebaldi 1998], [Barone & Tebaldi 2000]: even in the presence of such strong symmetry, i.e. when all the n species are characterized by the same ecological parameters, the system is able to provide patterns in which the species are differentiated. Coexistence can appear also as dominance of one species on the others through a variety of forms, i.e. equilibria, periodic oscillations or even strange attractors. In this *symmetric case*, the existence of a family of invariant subspaces has been shown and a 4-dimensional model introduced, with n as a parameter. Such a reduced model is proven to give full account of existence and stability of the equilibria in the complete system. Correspondence between the reduced model and the complete one has been found for a large range of parameter values also in the time dependent regimes, even in the presence of strange attractors. Such striking reduction results, even with multiplicity of attractors, very useful in the study of competition phenomena involving a large number of species, are related to the symmetry properties of the system.

It was on the line to clarify this aspect that we have chosen to differentiate some species on the ground of both the characterizing parameters, carrying capacity and intrinsic growth rate [Lacitignola & Tebaldi 2003]. The analysis of the equilibria in (3) has been completely described according to the size of ecological advantage or disadvantage of the first species: the case $c_1 \ll c$ exhibits the richest variety of equilibria, which have been investigated in full detail in [Lacitignola & Tebaldi 2004], also describing the phenomenology after their destabilization. The existence of a certain class of invariant subspaces for system (3) allows, also in this case, the introduction of a 7-dimensional reduced model, where n appears as a parameter: striking reduction properties are therefore still maintained [Lacitignola & Tebaldi 2005].

In this study, we focus on some interesting aspects of time dependent regimes and provide an example of coexistence in the form of complicated alternance between chaotic behavior and periodic one, in both cases with multiplicity of attractors.

1.2.1. The Equilibria

Investigations on the structure and properties of the equilibria in (3) can be efficiently performed making use of the reduced model. By recalling the symmetry properties of the system, we remark that any solution in this reduced model corresponds in general to $(n-1)$ such solutions in the complete system (3). Choosing the time scale, without loss of generality it is assumed $r = 1$, observing that the condition $r_1 = 1$ means equal reproduction rates for all the species whereas $r_1 < 1$ or $r_1 > 1$ indicate that the first species reproduces respectively more slowly or faster than the remaining ones. In the reduced model we have at most five interior fixed points, i.e. with all non zero equilibrium densities X_i , depending on the parameter r_1 , c_1 and c , namely

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$$R : X_1 = v \quad X_i = X_h = X_h^v \quad v \neq X_h^v$$

$$S : X_1 = s_1 \quad X_i = X_h = X_h^{s_1} \quad s_1 \neq X_h^{s_1}$$

$$S^* : X_1 = s_2 \quad X_i = X_h = X_h^{s_2} \quad s_2 \neq X_h^{s_2}$$

$$B : X_i = b_1 \quad X_1, X_h = X_h^{b_1} \quad b_1 \neq X_1, X_h^{b_1}$$

$$B^* : X_i = b_2 \quad X_1, X_h = X_h^{b_2} \quad b_2 \neq X_1, X_h^{b_2}$$

As a consequence, in the complete system, we have the three internal equilibria R, S and S*

$$(v, X_h^v, \dots, X_h^v), (s_1, X_h^{s_1}, \dots, X_h^{s_1}), (s_2, X_h^{s_2}, \dots, X_h^{s_2})$$

the (n-1) equilibria B;

$$(X_1^{b_1}, b_1, X_h^{b_1}, \dots, X_h^{b_1}), (X_1^{b_1}, X_h^{b_1}, b_1, \dots, X_h^{b_1}), \dots, (X_1^{b_1}, X_h^{b_1}, \dots, X_h^{b_1}, b_1)$$

and the (n-1) equilibria B*;

$$(X_1^{b_2}, b_2, X_h^{b_2}, \dots, X_h^{b_2}), (X_1^{b_2}, X_h^{b_2}, b_2, \dots, X_h^{b_2}), \dots, (X_1^{b_2}, X_h^{b_2}, \dots, X_h^{b_2}, b_2)$$

where $2 < i < n$.

To characterize the equilibria, we report only the n-ple of X_i 's since $\alpha_{ij} = X_i X_j$ at equilibrium. We also stress that any critical point of (3) with one or more components $X_i = 0$ is not considered here since it is proven to be unstable for all the values of the parameters. While the structure of the equilibria is essentially the same as in the symmetric case, their features depend both on the first species level of differentiation, the ecological conditions of the remaining species and their stability properties on the adaptation parameter T.

1.3. Complex Behavior in the Time Dependent Regimes

In this section we focus on the adaptive competition among four species and discuss an interesting example of complex behavior which arises in the time dependent regimes as an effect of adaptation. We consider the following intervals for the relevant parameters: $0.1 \leq r_1 \leq 3.5$, $0.01 \leq c_1 \leq 0.2$, $0.2 \leq c \leq 0.8$, $0 < T < 180$.

The equilibria for system (3) are represented in Figure 1, where the parameter plane cr_1 remains divided into four regions [Lacitignola & Tebaldi 2004].

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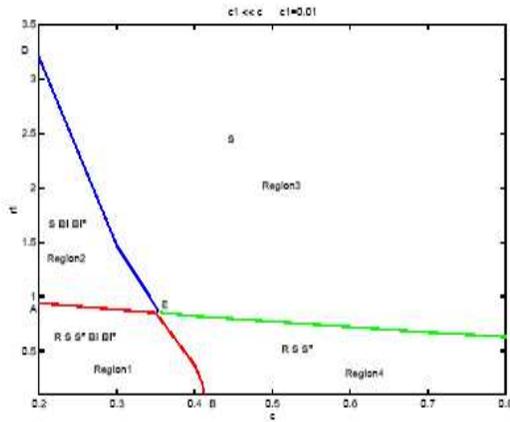


Figure. 1. The equilibria for the case $c_1 \ll c$, $c_1 = 0.01$.

Region1 has the richest phenomenology, in particular after the equilibria B_i 's have become unstable [Lacitignola & Tebaldi 2006]. We recall that the B_i 's are *coexistence* equilibria with a strong dominance of the i -species and, in this region, they lose stability at $T = T_B^*(c, r_1)$ either by supercritical or subcritical Hopf bifurcations.

The case $c = 0.35$ provides a variety of interesting dynamical patterns: for $T > \approx T_B^*$ and initial conditions near B_i , according to the value of r_1 , it is possible to have exclusion by the first species, i.e. the equilibrium S , or species coexistence in the form of periodic or complicated patterns. The most interesting phenomena are obtained when T is varied and $0.1 < r_1 < 0.42$; the case $r_1 = 0.2$ is chosen as representative of the above range and results are presented of investigations in the time dependent regimes, after destabilization of the equilibrium B_2 . For this range of the parameter values, such equilibrium loses its stability at $T = T_B^*$ via subcritical Hopf bifurcation and, as in the Lorenz system, for a set of initial conditions near B_2 , the system exhibits complicated behavior showing a chaotic attractor surrounding this unstable fixed point. In Figure 2 the chaotic attractor is shown for $T > \approx T_B^*$, i.e. $T = 26.5$

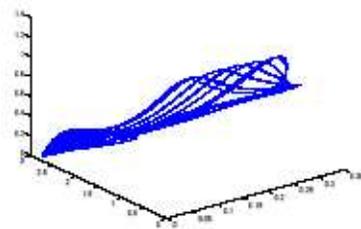


Figure. 2. The strange attractor in the (X_1, X_2, X_3) phase space for the case $c = 0.35$, $r_1 = 0.2$ and $T = 26.5$.

Increasing further the value of the parameter T , a stable order-7 cycle is found, where

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we denote as order- m cycle, a periodic solution having m loops around B_2 . Such cycle persists up to $T=29.3$ when it is replaced by a chaotic attractor, Figure 3.

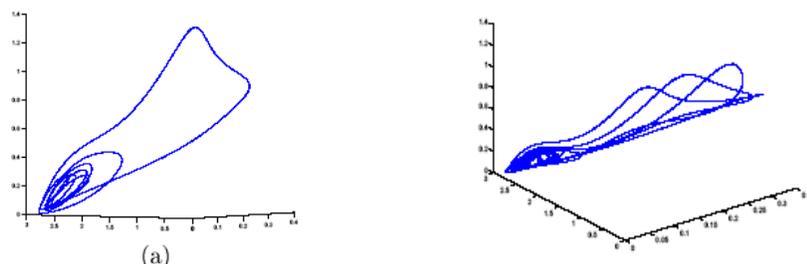


Figure 3. Projection in the (X_1, X_2, X_3) phase space (a) The order-7 cycle at $T=28.9$ (b) The chaotic attractor at $T=29.3$

At $T=29.5$ such an attractor leaves place to a stable order-6 cycle, which persists up to $T=30.5$, when a chaotic attractor is found, Figure 4.

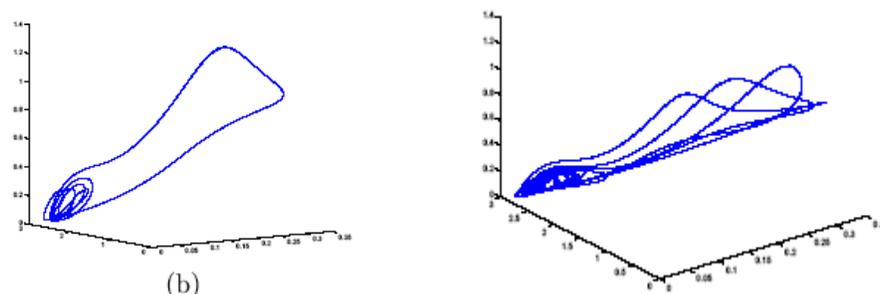


Figure 4. The order-6 cycle at $T=29.5$, and the chaotic attractor at $T=30.5$

This phenomenology reveals an interesting alternance of chaotic and periodic windows which are strictly linked to each other. Progressively increasing the value of T , the shape of the cycle is changed by removing, step by step, a loop around B_2 and equivalently the period decreases because of the disappearance of a spike. We show the occurrence of such an alternance up to the 4-order cycle, Figure 5; investigations are still in progress to clarify the system behavior when T is furtherly increased, also with the use of continuation analysis tools. Figure 3-Figure 5 provide an interesting example of a period-adding phenomenon, as reported in [Ott 1993], when read for T decreasing, strictly related to the chaotic windows.

The behavior described above has been found making use of the reduced model which considerably diminish the computational effort required. In all cases, persistence of the results for the complete model has been checked; as a consequence, three either cycles or strange attractors of the kind shown, are present in the system, obtained taking initial conditions close to each equilibrium B_i , $i=2, \dots, 4$.

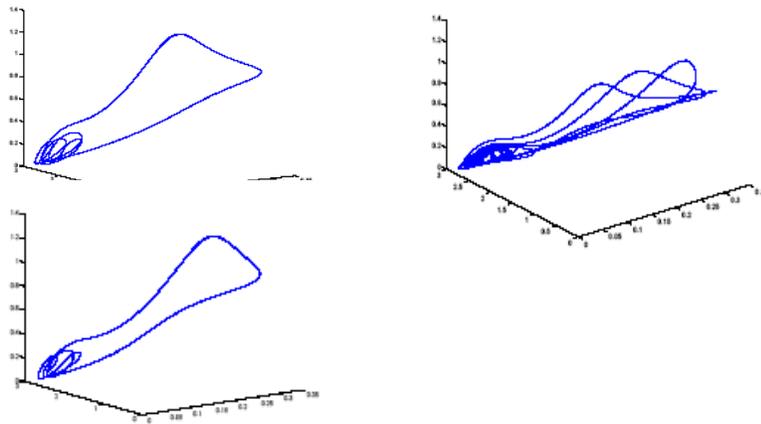


Figure 5. The order-5 cycle at $T = 31.1$, the chaotic attractor at $T = 31.7$ and the order-4 cycle at $T = 33$

The symmetry of the equilibrium B_i is however maintained also in the time-dependent regimes and in fact, eventually after a transient, $X_j(t) = X_i(t)$, $j \neq 1, i$ with striking properties of (partial) synchronization, taking place even in chaotic regimes. An interesting point under investigation is the eventual breaking of such symmetries, with loss of the related synchronization properties.

1.4. Conclusions

We have studied a competitive n -species Lotka-Volterra system with behavioral adaptation in which one species is differentiated with respect to the others by carrying capacity and intrinsic growth rate. A 7-dimensional reduced model is obtained, where n appears as a parameter, which gives full account of existence and stability of equilibria for the complete system and is also effective in describing the time dependent regimes for a large range of parameter values. Such a reduced model can be very useful for the study of adaptive competition involving a large number of species since the computational effort required is highly reduced.

We have presented interesting aspect of the phenomenology for certain values of the carrying capacities, c and c_1 , and the intrinsic growth rate r_1 , when the parameter T , characterizing behavioral adaptation, is varied. According to the values of the parameter r_1 , we have found, as expected, exclusion by the most advantaged species as one of the possible outputs. However, because of adaptation, coexistence among the species is also possible and in different forms, equilibria, periodic oscillations or even strange attractors. This aspect is interesting because it takes care of one of the main critics to the classical competitive Lotka-Volterra systems, namely the fact that they lead to exclusion of species far more often than observed. Furthermore, the complex phenomenology presented here, also allows to make contact with the varied behavior observed in nature, especially when the number of species with relevant interactions is not very small. In this respect it is interesting to point out that the results presented

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were qualitatively confirmed when a small amount of noise was added to the carrying capacities of the species and further investigations on this line are planned.

The problem of general networks with logistic dynamics on each node and adaptive interactions among them is also being addressed, in particular to investigate if the reduction properties discussed here will persist.

Finally, going back to Goodwin's model of economic growth cycles, the introduction of behavioral adaptation in the same line discussed here [Colacchio, Sparro & Tebaldi, submitted], has substantially extended the validity of the model and provided a rich phenomenology more related to actual historical data [Harvie 2000].

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