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The dynamics of two diffusively coupled, identical Lotka-Volterra patches.

Summary

The idea that fluctuations in population densities are less in a metapopulation than in an isolated single population is based on the presumption of asynchrony of local dynamics. To scrutinize the validity of this presumption we formulate a model for a metapopulation consisting of two identical patches. Each patch is inhabited by a prey and a predator who interact according to the Lotka-Volterra model and migrate randomly. We investigate the stability of synchronous solutions i.e. solutions in which the densities in both patches are equal. Large amplitude synchronous solutions can be unstable for low prey migration rates and intermediate predator migration. In orbits starting close to these unstable solutions the differences between local densities can increase. In the long run all orbits with positive initial conditions converge to a synchronous orbit. However, through the temporal asynchrony of local dynamics, the fluctuations in the two patch Lotka-Volterra metapopulation are reduced compared to those of an isolated population. This offers a mechanism for the regulation of predator and prey populations without density dependence at the level of the individual.

6.1 Introduction

Metapopulation theory describes a population that lives in a collection of habitat patches. The local populations that occupy these patches interact through migration. Local populations can go through cycles of colonization and extinction. When the cycles of extinction and colonization are not synchronized, patches that become empty because the local populations that occupied them went extinct, can be recolonized from still existing local populations. Through this mechanism a metapopulation is likely to persist for much longer periods than a single large population.

Predator and prey populations that live and interact in an ensemble of patches can exhibit metapopulation dynamics. Each local predator-prey population itself is capable of exhibiting fluctuations. When these local populations fluctuate asynchronously the peaks in the densities of some local populations coincide with the troughs in the densities of some other local populations. Such asynchronous dynamics has empirically been observed in predator-prey metapopulations (Nachman, 1991; Van de Klashorst *et al.*, 1992). A metapopulation with asynchronous local dynamics therefore not only is more persistent than a single large population, but on a large spatial scale also fluctuates less.

Differences in local densities are intrinsic to asynchronous local dynamics. Lasting differences between local densities in a system of patches coupled through migration may seem unexpected: how can migration, which will tend to level out differences, at the same time enhance differences? Turing (1952) was the first to demonstrate the existence of such diffusive instabilities. Turing's equations describe a spatial biochemical system. Without diffusion the system settles in a stable equilibrium. The combined forces of diffusion and the chemical reactions can make this equilibrium unstable. The spatial symmetry in the coupled system is broken and differences between the local concentrations persist. Predator-prey systems can behave like Turing's system and in spatial predator-prey systems diffusive instabilities can occur (Segel & Jackson, 1972).

The existing work on diffusive instabilities focuses on systems which settle in a stable equilibrium without diffusion. A local predator-prey population, however, can settle on a limit cycle in the absence of migration. For metapopulations, the relevant question is thus whether or not the state in which the local populations cycle in synchrony is diffusively unstable. Despite a vast literature on spatial predator-prey systems, diffusive instabilites in predator-prey systems, which oscillate when left to themselves, has received hardly any attention until recently. Last years a number of papers appeared on coupled oscillating ecological systems. Gyllenberg *et al.* (1993) and Hastings (1993) demonstrated the existence of asynchronous local oscilations in a system of two coupled logistic maps and Adler (1993) showed that differences between local densities can persist in a system of two coupled host-parasitoid populations.

In this paper we explore the dynamics of the simplest possible model for a continuous time predator-prey metapopulation: a Lotka-Volterra system in two identical patches. Although this model has a respectable history (Comins & Blatt, 1974; Murdoch & Oaten, 1975), the stability of its synchronous solutions, and that of the spatially constant solutions of its continuous space analogue (see Levin, 1976) for a review) to our knowledge, never has been studied in detail. We will show that synchronous oscillations can be unstable and that a temporal increase of asynchrony between local population densities can occur. Moreover, we will show that population densities in one isolated patch can fluctuate stronger than those in the corresponding two patch "metapopulation".

The two patch Lotka-Volterra model has also received attention to examine the stabilizing effect of predator aggregation on (meta)population dynamics (Godfray & Pacala, 1992; Murdoch *et al.*, 1992; Nisbet *et al.*, 1992). For a single species it has been shown that migration can reduce the fluctuations in the densities (allen *et al.*, 1993). For predator prey sytems this question is still for a good deal open. The two patch Lotka-Volterra model has the advantage over many other models for predator aggregation that it describes aggregation at a behavioral, rather than at a phenomenological level. Our results show that predator aggregation can indeed dampen the fluctuations in densities through an increase in asynchrony.

The work presented in this paper has significance beyond metapopulations: a two patch system is a coarse discretisation of a spatial system. When in the two patch situation symmetry can break, it can happen as well in a full spatial predator-prey system. Symmetry breaking gives rise to spatial patterns. Predator-prey systems in a homogenous environment can display spatial patterns (Hassell *et al.*, 1991; Comins *et al.*, 1992; Boerlijst *et al.*, 1993; Wilson *et al.*, 1993). These populations seem to be regulated rather through the spatial interactions than through density dependence at the level of the individual (De Roos *et al.*, 1991). Here we will demonstrate that the spatial interactions can regulate predator-prey populations even in the absence of individual density dependence.

6.2 The two patch Lotka-Volterra model

The Lotka Volterra model describes a system of interacting prey and predator populations. After a scaling the model corresponds to:

$$\begin{aligned} \tfrac{dN}{dt} &= rN - NP \\ \tfrac{dP}{dt} &= NP - \mu P \end{aligned} \tag{6.1}$$

N represents the density of the prey, P the density of the predator, r is the the growth rate of the prey population in absence of predators and μ the death rate of predators. The phase portrait of the Lotka-Volterra system consists of a family of closed orbits around a neutrally stable equilibrium. We will study the dynamics of a system of two identical coupled patches, in which the dynamics within a patch is described by (6.1). The two patches are coupled through migrations.

For the system of two patches the equations read:

$$\begin{aligned} \frac{dN_i}{dt} &= rN_i - N_iP_i + d_n(N_j - N_i) \\ \frac{dP_i}{dt} &= N_iP_i - \mu P_i + d_p(P_j - P_i) \end{aligned} \qquad i,j \in \{1,2\}; \quad i \neq j, \tag{6.2}$$

where N_i and P_i denote the density of, respectively, the prey and the predator in patch i. The constant d_n is the migration rate of the prey and d_p the migration rate of the predator.

6.3 The stability of the synchronous solutions

When the densities of both prey and predator are equal in both patches the effects of migration cancel and the densities are not affected by migrations. Since the patches are equal the densities will then forever remain equal. Hence, the diagonal $\{(N_1, P_1, N_2, P_2) \in \mathbb{R}_+^4 | N_1 = N_2, P_1 = P_2\}$ is invariant and contains all synchronous solutions of (6.2). The dynamics on it are those of the Lotka-Volterra equations (6.1): a family of closed orbits surrounds a neutrally stable equilibrium point. This equilibrium is the unique positive equilibrium of (6.2) (Murdoch *et al.*, 1992). From the invariance of the diagonal it follows that the positive equilibrium has two purely imaginary eigenvalues, as the equilibrium of the Lotka-Volterra model has. The other two eigenvalues always have negative real part (Nisbet *et al.*, 1992; see also Appendix).

We will next concentrate on the stability of the synchronous periodic orbits that lie on the diagonal. The stability properties of the periodic orbits is determined by their Floquet multipliers (Hartman, 1964), much like the stability of equilibria of discrete time dynamical systems is determined by the multipliers. A periodic orbit is unstable when the modulus of at least one multiplier exceeds one and stable otherwise. Each orbit of the two patch Lotka-Volterra model has four Floquet multipliers. To determine the value of the Floquet multipliers we linearise (6.2) in the neighbourhood of the diagonal (see Appendix). The linearised system consists of two decoupled sets of equations. One set describes the linearised dynamics within the diagonal, the other set the linearised dynamics near the diagonal. Within the diagonal the dynamics are given by (6.1). With the two equations of (6.1) two multipliers are associated. One of these Floquet multiplier is one since we consider a closed orbit and from the existence of a constant of motion for the (single patch) Lotka-Volterra model it follows that the second Floquet multiplier also has value one. The value of the remaining two Floquet multipliers can be derived from the linearisation near the invariant diagonal, which for the two patch Lotka-Volterra model takes the form (see Appendix):

$$\frac{d\delta(t)}{dt} = \begin{pmatrix} r - P(t) - 2d_n & -N(t) \\ P(t) & N(t) - \mu - 2d_p \end{pmatrix} \delta(t). \tag{6.3}$$

where $N(t)$ and $P(t)$ are given by (6.1). Since $N(t)$ and $P(t)$ are periodic in t, (6.3) is a Floquet problem.

The sum of the Floquet exponents is the time averaged trace of the Floquet matrix (Hartman, 1964). The time averages over a period of the prey and predator densities in the Lotka-Volterra model are, respectively, μ and r. The sum of the exponents of any orbit of the two patch Lotka-Volterra model is therefore $-2(d_n + d_p)$. The product of the multipliers thus equals $\exp(-2(d_n + d_p)\tau)$, with τ the period of $N(t)$ and $P(t)$. Useful in this context is also the following observation: when the migration parameters both are increased by α, all Floquet exponents decrease by α. Therefore, a necessary condition for orbits to be unstable with positive migration rates is a positive Floquet exponent when one migration rate equals zero. Once the multipliers are known when one of the migration rates is equal to zero, the multipliers of (6.2) with both migration rates positive can be computed directly. This motivates the choice below of one migration rate equal to zero.

Direct calculation of the Floquet multipliers from (6.3) requires an expression for at least one eigenfunction, which, despite considerable effort, we could only find in two specific and, unfortunately, not very interesting cases. We therefore numerically computed the Floquet multipliers. All computations were done with the software package "LOCBIF" (Khibnik *et al.*, 1993).

6.4 Main results

Since our results were mainly derived from numerical studies we will present them in a series of figures. Figure 6.1 gives the modulus of the multipliers as a function of the period. The phase portrait of the Lotka-Volterra system consists of a family of closed orbits. The period of the closed orbits is monotonic

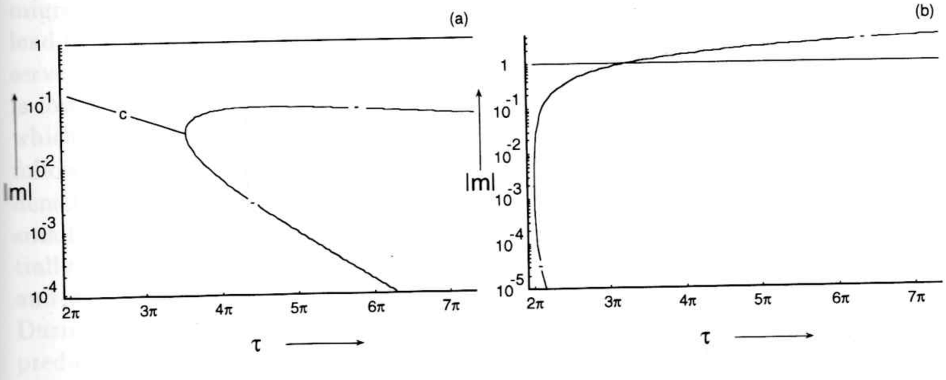

Figure 6.1: The moduli of the multipliers of (6.3) as a function of the period τ of a solution of (6.1). Lines indicated with "c" correspond to complex multipliers, lines indicated with "-" to negative real multipliers. Close to the equilibrium the period is approximately $2\pi(\sqrt{\mu r})^{-1}$. (a) Parameters: $\mu = 1$, $r = 1$, $d_n = 0.3$, $d_p = 0$. (b) With parameters: $d_n = 0$, $d_p = 1$.

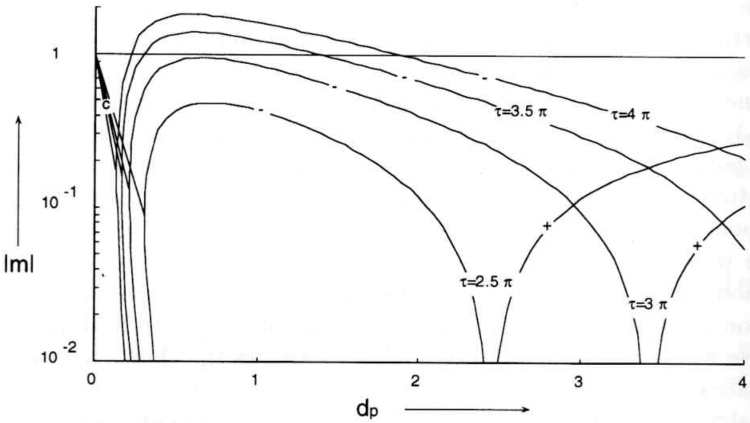

Figure 6.2: The moduli of the multipliers of (6.3) as a function of the predator migration rate d_p for various values of τ with parameters: $\mu = 1$, $r = 1$ and $d_n = 0$. Lines indicated with "c" correspond to complex multipliers, lines indicated with "+" to positive multipliers and lines indicated with "-" to negative multipliers.

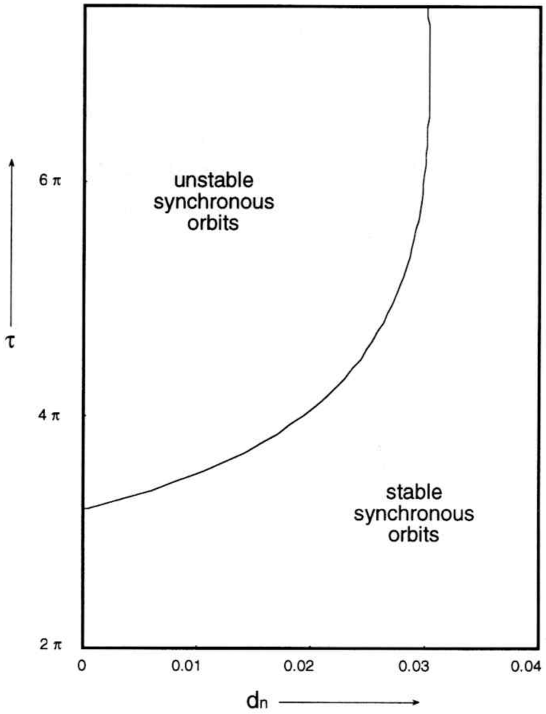

Figure 6.3: The period of the critical cycle (the synchronous periodic orbit with multiplier -1) as function of the prey migration rate d_n. Parameters: $\mu = 1$, $r = 1$ and $d_p = 0.75$.

(Rothe, 1985; Waldvogel, 1986) and thus forms a convenient index for the synchronous orbits. In Figure 6.1a the predator migration rate is set to zero. The moduli of the synchronous orbits attract. In Figure 6.1b the prey migration rate is zero. Now the modulus of one of the multipliers crosses 1 (in all studied cases this happened when a multiplier had value -1). At the point of crossing a critical cycle exists that neither attracts nor repels. The cycles with smaller period are stable whereas the ones outside are unstable. Since the period of the synchronous orbits increases with amplitude the stable synchronous orbits lie within a disc bordered by the critical cycle and the unstable ones outside.

To illustrate the dependence of the stability of synchronous orbits on predator migration, Figure 6.2 gives the moduli of the multipliers as function of the predator migration rate for a number of periodic solutions. There is a minimal period for synchronous orbits to lose stability. Figure 6.3 gives the period of the critical cycle, which separates the stable and unstable limit cycles, as a function of d_n. For cycles with a large enough period there exists a window in d_p for which instability can occur. When there is either too much or too little predator migration the periodic orbits are stable. The critical cycle increases rapidly with d_n. For large values of the period the numerical results are unclear, the results from the continuation procedure used to produce Figure 6.3 suggest that the stability boundary curves back slightly for high values of the period. Direct numerical integration gives contradictory results; unstable synchronous solutions seem to exist for large periods on the right side of the boundary depicted in Figure 6.3.

Apparently the synchronous orbits are always stable when the prey migration rate exceeds a certain value. To get a more complete view of the regions where unstable synchronous orbits are possible we continued the critical cycle in the d_p, d_n parameter space (Figure 6.4). Unstable orbits are possible for small prey migration rates and intermediate predator migration rates. Figures 6.3 and 6.4 lead us to propose a possible mechanism for this diffusive instability. First we observe that large Lotka-Volterra cycles consist of a part where the predator density is low and the prey density grows almost exponentially, followed by a phase in which the predator density increases rapidly on expense of the prey density, to be followed by an almost exponential decay of the predator density, while the prey density is low. During the phase in which the prey density increases rapidly, a small difference in the prey densities between patches increases almost exponentially if prey migrates little or not. The conversion of prey into predator is fast and will convert differences in prey density into differences in predator density. During the almost exponential decay of the predator density the differences in predator density will decrease. For large predator migration rates the differences will decrease fast and any initial differences will disappear.

The patch that in the beginning had more prey now has more predators, who eat prey. Hence at the beginning of the next period of nearly exponential prey growth this patch will start with less prey (which explains for a negative multiplier). For very small predator migration there is not enough coupling between the patches to bring about instabilities. Hence, only for intermediate

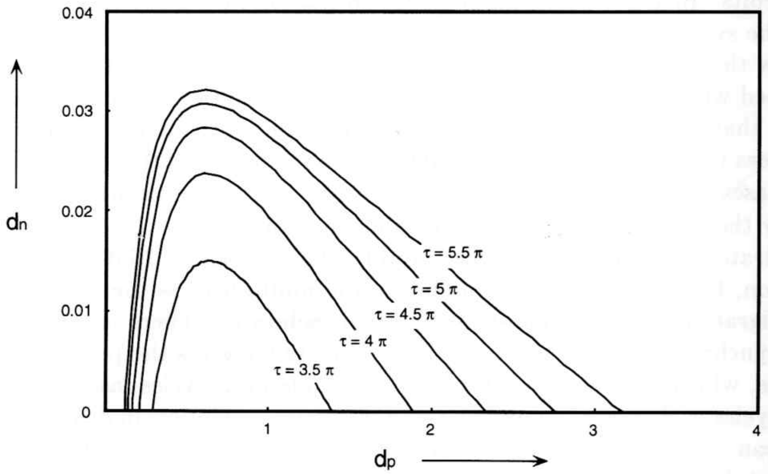

Figure 6.4: Stable and unstable domains of various synchronized orbits of (6.2) (parametrized by τ, see Figure 6.1). (a) In the d_p, d_n parameter space. A synchronized orbit with period τ is unstable for d_p, d_n under the graph and stable for combinations above the graph. Parameters: $\mu = r = 1$.

predator migration rates diffusive instability is possible.

As can be seen from (6.3), $2d_n < r$ is a necessary condition for prey differences to build up. Although we never observed unstable cycles when this condition was not fulfilled, it seems that only for predator migration rates far below $\frac{1}{2}r$ diffusive instabilities are possible. When the explanation given above truly describes the mechanism by which differences can increase, unstable synchronous orbits should occur more readily for a shorter average predator lifetime. This shortens the time in which the differences can fade out due to predator migration. Figure 6.5 shows that this is indeed the case. The window in the predator migration rate for which unstable synchronous orbits are possible, widens with increasing predator death rate.

For the continuous space Lotka-Volterra model with zero flux boundary conditions and positive migration rates it is well known that in the end all spatial differences will disappear; all solutions converge to a spatially constant solution that still can vary in time (Murray, 1975). A similar result holds for the two patch Lotka-Volterra model:

Theorem 1 *All solutions of (6.2) with positive initial conditions and at least one positive migration rate become synchronized.*

Proof: The functional:

$$V_i(N_i, P_i) = N_i - \mu \ln N_i, + P_i - r \ln P_i > 0,$$

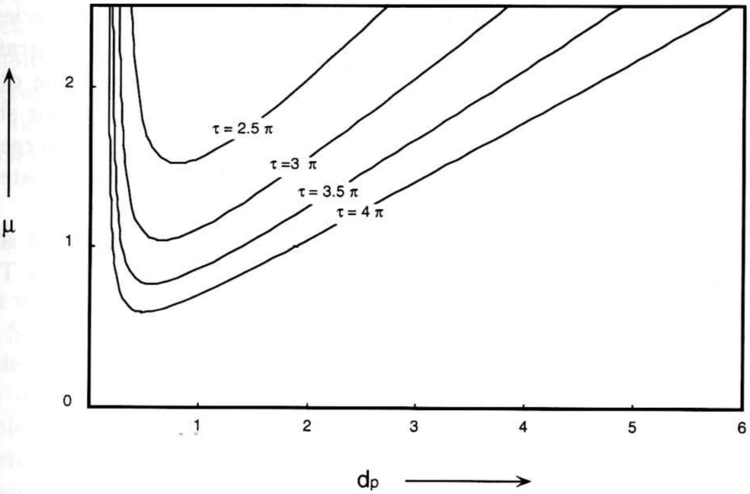

Figure 6.5: (b) In the d_p, μ parameter space. A synchronized orbit with period τ is unstable for d_p, μ combinations above the graph and stable for combinations below. Parameters: $r = 1.0$, $d_n = 0$.

which is defined for $N_i, P_i > 0$, is a constant of motion for an isolated Lotka-Volterra patch. Consider

$$V = V_1 + V_2$$

Along orbits of the two patch Lotka-Volterra model V changes according to:

$$\frac{dV}{dt} = -\mu d_n \frac{(N_1 - N_2)^2}{N_1 N_2} - r d_p \frac{(P_1 - P_2)^2}{P_1 P_2} \leq 0$$

and hence it serves as a Lyapunov function for the two patch Lotka-Volterra model.

For both migration rates positive $dV/dt = 0$ if and only if $N_1 = N_2, P_1 = P_2$ and hence the ω-limit set of any orbits with positive initial conditions consists of synchronous solutions. When $d_n = 0, d_p > 0$ the ω-limit sets of all orbits with positive initial conditions are contained in the invariant sets of $\{(N_1, P_1, N_2, P_2) \in \mathbb{R}^4_+ | P_1 = P_2\}$. When $P_1 = P_2$ also $dP_1/dt = dP_2/dt$ from which follows directly that $\{(N_1, P_1, N_2, P_2) \in \mathbb{R}^4_+ | N_1 = N_2, P_1 = P_2\}$ is the only invariant set in $\{(N_1, P_1, N_2, P_2) \in \mathbb{R}^4_+ | P_1 = P_2\}$ and hence all orbits with positive initial conditions asymptotically become synchronized. For $d_n > 0, d_p = 0$ it can by proven that all solutions become synchronized by a similar argument. □

As a side remark we note that the cases where initially a species is absent in one or both of the patches are not covered by Theorem 1. It can be easily seen, however, that when prey is initially absent in both patches, solutions will converge to a state with all patches empty. When predators are initially absent the prey will grow exponentially. The difference between the prey densities will then increase iff $2d_n < r$. It is also obvious that when one of the species is initially missing in one of the patches all solutions synchronize when the migration rates are positive. When one of the migration rates is positive and the other zero, a patch can remain unoccupied by one of the species. Simulations show exponential prey growth when no side equilibrium is possible, and convergence to an equilibrium when it exists. Since we are mainly concerned with the existence of unstable synchronous solutions these cases are of minor interest here.

At first sight the existence of unstable synchronous closed orbits might seem to contradict the fact that all orbits converge to synchronous closed orbits. That

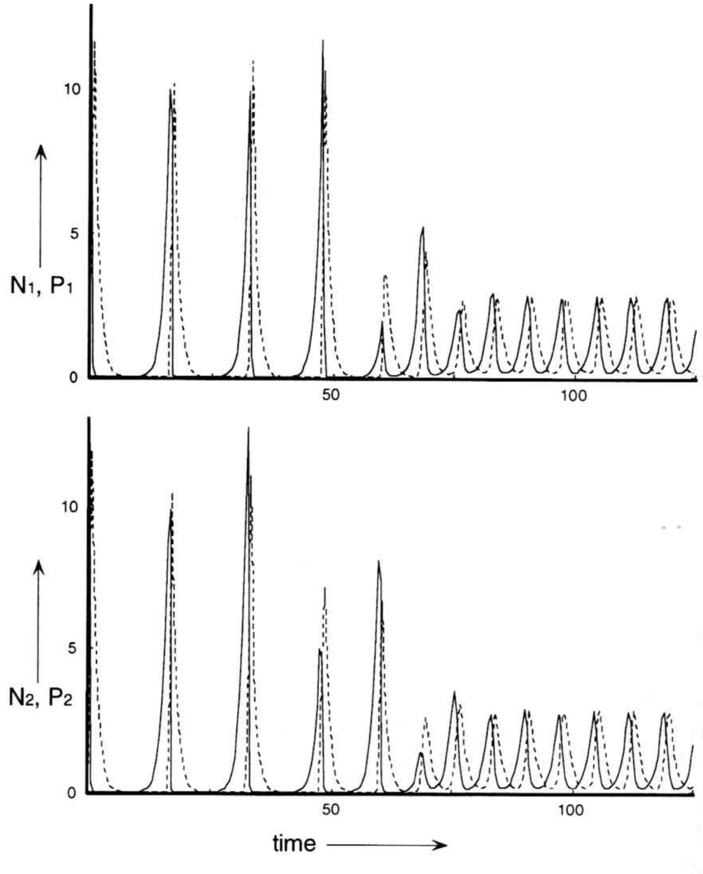

Figure 6.6: A solution of (6.2) with parameters: $\mu = r = 1$, $d_n = 0$, $d_p = 1$ and initial conditions: $N_1(0) = 12$, $P_1(0) = 1$, $N_2(0) = 12.5$, $P_2(0) = 1$. The first figure gives predator and prey densities in patch 1 versus time, the second figure the densities in patch 2. Drawn lines represent prey densities, dashed lines predator densities.

this contradiction is only apparent is shown in Figure 6.6. A solution of the two patch Lotka-Volterra model that starts close to an unstable synchronous orbit initially shows increasing differences in densities between the patches. Later these differences disappear and the orbit converges to a synchronous cycle. Note that the amplitude of the oscillations of the synchronous orbit reached in the end are much smaller than those in the beginning.

6.5 Discussion

It is well known that spatial differences disappear in spatial Lotka-Volterra models. Stability analysis of the synchronous cycles in the two patch Lotka-Volterra model with identical patches reveals that, as Steele (1974) conjectured correctly, this does not imply that every synchronous or spatially constant solution, is stable. For suitably chosen migration rates the differences in densities between patches can first increase, and only disappear after the oscillations in the total densities have damped sufficiently.

For a spatially continuous spatial Lotka-Volterra model we expect the same to hold, since a two patch system is nothing more than a discretisation of space in two parts. One can then ask whether this behaviour is robust against changes in the predator-prey interactions. The Lotka-Volterra model is structurally unstable. When the patches still are identical, small changes in the predator-prey interaction terms will therefore qualitatively change the behaviour of synchronous solutions. However, under a small change in the equations the connections from synchronous solutions with a high amplitude to synchronous solutions with a smaller amplitude persist, giving rise to complex dynamics. We will demonstrate this in a forthcoming paper. The complex dynamics can be expected to persist under small differences between the patches.

The highly idealized conditions of the Lotka-Volterra model will never be met in real populations. In nature there will always be small fluctuations in the environment, demographic stochasticity or some density dependence. Environmental fluctuations, for instance, can cause the dynamics to "drift" through phase space, causing an irregular sequence of highs and lows in the densities (Fig. 6.7a). In the two patch Lotka-Volterra model eventually all spatial differences will vanish and all orbits converge to a bounded set of synchronous periodic orbits. When drift is imposed on this system it will sooner or later exhibit oscillations with high amplitudes. As shown, periodic orbits with high amplitudes can be diffusively unstable. Spatial differences then amplify and cause a reduction of the fluctuations of the metapopulation. Through the interplay of spatial interactions and local unstable dynamics spatial differences and the asynchrony of local dynamics can be maintained. Local populations, which oscillate when isolated, thus possess a mechanism that can asynchronize local dynamics and that keeps the fluctuations bounded (Fig. 6.7b). This supports one of the assumptions of metapopulation theory and illustrates how the oscillations of a metapopulation can be reduced compared to those of an isolated population.

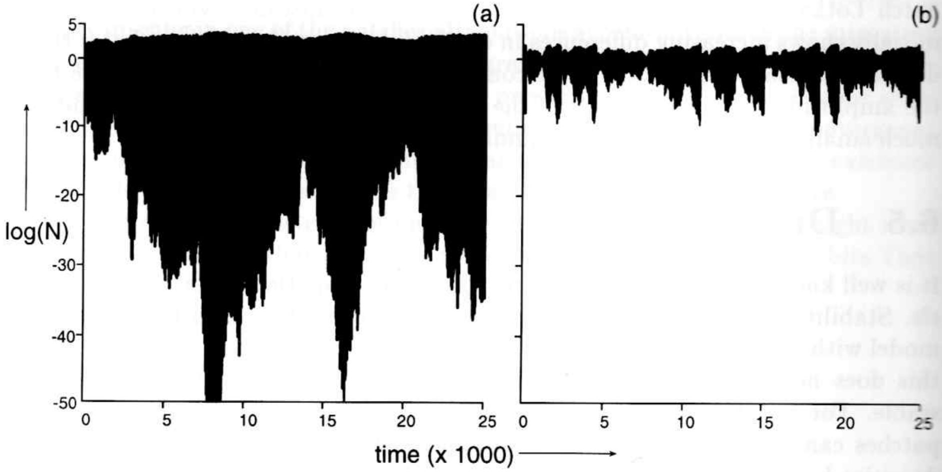

Figure 6.7: (a) The logarithm of the prey densities of the Lotka-Volterra model (6.1) versus time with random noise on the predator death rate μ. The model shows unbounded drift and attains very low densities. Parameters: $r = 1$, $\mu = 1 \pm 0.1$. (b) The logarithm of the average prey densities $N = 1/2(N_1 + N_2)$ of the two patch Lotka-Volterra model (6.2) versus time with identical noise imposed on the predator death rate μ as in (a). Although the densities still drift they are bounded away from zero. Parameters as in (a), $d = 0.7$.

For the fact that the dynamics can drift away to infinity, the Lotka-Volterra model has been discarded as a true representation of real populations (e.g. May, 1972 and 1981). The observations in this paper show that this drift can be bounded when spatial interactions are taken into account (Fig. 6.7). This sheds a new light on some old ecological questions. The unbounded solutions of the Lotka-Volterra model with drift have urged ecologists to seek for density dependent mechanisms that regulate natural predator-prey populations at an individual level. A spatial analogue of the same model shows that population dynamics can be bounded through spatial interactions without density dependence being measurable at an individual level.

Acknowledgements

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6.6 Appendix: On the determination of the stability of synchronous solutions

Let the dynamics in an isolated ecosystem be determined by:

$$\frac{dX}{dt} = F(X) \tag{6.4}$$

where $X = (x_1, ..., x_n)^T$ represents the state of the ecosystem. The ecosystem's components x_i can, for instance, correspond to species or different life stages of a species. The function $F(X) = (f_1(X), ..., f_n(X))^T$ is a vector valued function of X.

When two patches, whose dynamics when isolated are given by (6.4), are coupled through migration, their dynamics are given by:

$$\left\{ \begin{array}{ll} \frac{dX}{dt} & = F(X) + M(Y - X) \\ \frac{dY}{dt} & = F(Y) + M(X - Y) \end{array} \right. \tag{6.5}$$

where X and Y denote the states of the respective patches. The matrix M has the migration rates of the respective ecosystem components m_i on its diagonal and all other elements are zero.

Synchronous solutions are those solutions for which $X(t) = Y(t)$ for all t. We will study the stability properties of these synchronous solutions. To facilitate analysis we introduce the new variables:

$$S = \frac{1}{2}(X + Y)$$

where S is an $n-$dimensional vector representing the average density of the ecosystem components over the system of two patches, and

$$\Delta = X - S = \frac{1}{2}(X - Y)$$

where Δ is an $n-$dimensional vector representing the differences between the density in a patch and the average density of the ecosystem.

Now S changes over time, according to

$$\frac{dS}{dt} = \frac{1}{2}\left[F(S + \Delta) + F(S - \Delta)\right] \tag{6.6}$$

and Δ according to:

$$\frac{d\Delta}{dt} = \frac{1}{2}\left[F(S + \Delta) - F(S - \Delta)\right] - 2M\Delta \tag{6.7}$$

Obviously, the $n-$dimensional subspace $\Delta = 0$, which contains all synchronous solutions, is invariant. To study the stability properties of a synchronous solution $S = \tilde{S}$, $\Delta = 0$ we expand (6.6) and (6.7) around $\{(S, \Delta) \in \mathbb{R}^{2n} | S = \tilde{S}, \Delta = 0\}$:

$$\begin{aligned} \frac{dS}{dt} &= \frac{1}{2}\left[2F(\tilde{S}) + 2DF(\tilde{S})(S-\tilde{S}) + O((S-\tilde{S})^2 + \Delta^2)\right] \\ \frac{d\Delta}{dt} &= \frac{1}{2}\left[2DF(\tilde{S})\Delta + O((S-\tilde{S})^2 + \Delta^2)\right] - 2M\Delta, \end{aligned}$$

where

$$DF(X) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \cdots & \frac{\partial f_1}{\partial x_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial x_1} & \cdots & \frac{\partial f_n}{\partial x_n} \end{pmatrix}.$$

After dropping the higher order terms and substituting $\sigma = S - \tilde{S}$ and $\delta = \Delta$ we obtain the linearised system:

$$\frac{d\sigma}{dt} = DF(\tilde{S})\sigma \quad (6.8)$$

$$\frac{d\delta}{dt} = \left(DF(\tilde{S}) - 2M\right)\delta. \quad (6.9)$$

In the linearised system σ and δ are decoupled. Hence a synchronous solution is stable if and only if $\sigma = 0$ is a stable solution of (6.8) (which implies that $\tilde{S}$ is stable solution of (6.4)) and $\delta = 0$ is a stable solution of (6.9). When $\tilde{S}$ is a fixed point the synchronous solution is stable iff both the matrices $DF(\tilde{S})$ and $DF(\tilde{S}) - 2M$ do not have positive eigenvalues. When $\tilde{S}$ is periodic it is stable when the moduli of the Floquet multipliers of systems (6.8) and (6.9) do not exceed unity. In all other cases the stability of $\tilde{S}$ can be assessed from the dominant Lyapunov exponents of (6.8) and (6.9).

In general there are no methods to determine the stability of (6.9) directly from (6.8), except when all ecosystem components have identical migration rates. This is, for instance, the case in coupled chemostats. Then, (6.9) can be transformed in (6.8) by substituting $\sigma(t) = \exp(mt)\delta(t)$, where m is the migration rate and the stability of (6.8) is a necessary and sufficient condition for the stability of a synchronous solution. A corollary is that the synchronous solutions of a system of two patches, in which the dynamics in a single patch is described by a single continuous variable (so that the two patch system has a single migration rate) cannot be destabilized by diffusion.