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Stability of a stochastic predator-prey system (**)

dedicated to the memory of Giulio di Cola

1 - Introduction

We consider the following Lotka-Volterra predator-prey model

$$(1) \qquad \begin{cases} dx_t = [rx_t(1-x_t) - qx_t y_t]\, dt \\ dy_t = [cqx_t y_t - uy_t]\, dt \end{cases}$$

where x_t and y_t are the normalized biomass size at time t of prey and predator respectively; r, c, u are physiological parameters and q is a behavioural parameter. A more general system, whose (1) is a special case, describing the local dynamics of trophic interaction in an acarine predator-prey system has been studied in [**1**], in order to analyze the dependence of the steady states stability on physiological and behavioural model parameters. Parameters r, c, u are supposed known (being estimated under special assumptions, using demographic models of single species population), while the behavioural parameter q is considered as a control parameter.

The steady state solutions to (1) are ([**1**]):

- a null state $E_0 = (0, 0)$ where prey and predator are extinguished, which is unstable for any q;
- a non coexistence state $E_1 = (1, 0)$ where only predator is extinguished, which is stable if $q < \dfrac{u}{c}$ and unstable if $q > \dfrac{u}{c}$;

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- a coexistence state $E^* = \left(\frac{u}{qc}, \frac{r}{q}\left(1 - \frac{u}{qc}\right)\right)$, where predator and prey are both present, which exists and is stable if and only if $q > \frac{u}{c}$.

It can be shown that for any initial value, if $q < \frac{u}{c}$, then the solutions converge to E_1; if $q > \frac{u}{c}$, then they converge to E^*; therefore E_1 and E^*, when stable, are globally stable.

In the present work we suppose that the parameter q, due to his meaning of predator search efficiency, depends on the time t, fluctuating in an erratic way around an unknown mean value q_0. Assuming

$$dq_t = q_0\, dt + \sigma dw_t \tag{2}$$

where w_t is a Wiener process and σ is a positive constant, we transform (1) in the following stochastic model ([**6**])

$$\begin{cases} dx_t = [rx_t(1 - x_t) - q_0 x_t y_t]\, dt - \sigma x_t y_t\, dw_t \\ dy_t = [cq_0 x_t y_t - uy_t]\, dt + c\sigma x_t y_t\, dw_t . \end{cases} \tag{3}$$

The stability of the equilibrium solutions of (3) has been studied in [8] and [**2**], making use of Lyapunov exponents methods without determining a stability threshold for q_0. Here we determine stability conditions of the equilibrium solutions of (3) by means of a Lyapunov function and study how much the hypothesis (2) affects the qualitative character of the solutions as σ is varying.

This paper is organized as follows. In section 2 we recall a few results, useful in the sequel, on the stochastic stability of equilibrium solutions. In section 3, we study the stability of equilibrium solutions of system (3) by means of a Lyapunov function and observe that the degenerate solution E_0 is still unstable for any positive value of q_0 and σ, while the other degenerate solution E_1 is asymptotically stable when q_0 is less than a given threshold T_1 and unstable when q_0 is greater than a value T_2; T_1 and T_2 depend on σ. In section 4 numerical simulations of trajectories of the solutions of (3) confirm the analytical results obtained and concluding remarks can be found.

2 - Stochastic stability

We briefly recall definitions for the stability of equilibrium states of a stochastic differential equation and stochastic Lyapunov methods, introduced by Khasminskii ([5]). Consider an n-dimensional stochastic differential equation system

$$dX_t = f(t, X_t)\, dt + g(t, X_t)\, dw_t, \qquad t > t_0, \qquad X_{t_0} = x_0 \in \mathbb{R}^n \tag{4}$$

where $X_t \in \mathbb{R}^n$, f and g are n vector valued functions for $t \in [t_0, T]$, and w_t is a Wiener process. If the assumptions for the existence and uniqueness of the solution hold on every finite subinterval $[t_0, T]$ of $[t_0, \infty)$, then equation (4), for initial value $X_{t_0} = x_0 \in \mathbb{R}^n$, has a unique solution $X_t(t_0, x_0)$ on the entire interval $[t_0, \infty)$, called global solution.

Definition 1. *The stochastic process* $X_t \equiv \overline{X}$ *is a* stationary solution *of stochastic system* (4) *with initial condition* $X_{t_0} = \overline{X}$ *if*

$$f(t, \overline{X}) = 0\,, \qquad g(t, \overline{X}) = 0\,.$$

Without loss of generality, $\overline{X}$ *is taken to be zero and the stationary solution* $X_t \equiv 0$ *is said the* trivial solution.

Definition 2. *The trivial solution* $X_t \equiv 0$ *is said to be*

1. stable in probability *if for every* $\varepsilon > 0$ *and* $s \geqslant t_0$

$$\lim_{x \to 0} P\left(\sup_{t \in [s, \infty)} |X_t(s, x)| \geqslant \varepsilon \right) = 0\,. \tag{5}$$

The stability is said to be uniform *if the limit in* (5) *is uniform in* s.
If condition (5) *does not hold, then the trivial solution is said to be* unstable;

2. asymptotically stable *if it is stable in probability and moreover*

$$\lim_{x \to 0} P\left(\lim_{t \to +\infty} |X_t(s, x)| = 0 \right) = 1 \qquad s > t_0 \tag{6}$$

3. asymptotically stable in the large (*or globally*) *if it is asymptotically stable and moreover, for all* $x \in \mathbb{R}^n$

$$P\left(\lim_{t \to +\infty} |X_t(s, x)| = 0 \right) = 1\,. \tag{7}$$

The following theorem gives conditions for stability of stochastic systems in terms of Lyapunov functions.

Theorem 1. *Assume that there exists a function* $V(t, \xi) \in C^{1,2}$, $t > 0$ *and* $\xi \in \mathbb{R}^n$, *such that, for all* $|\xi| \leq k$ *with* k *positive constant,*

$$a(|\xi|) \leq V(t, \xi) \leq b(|\xi|) \tag{8}$$

where a *and* b *are continuous, positive definite functions on* $\mathbb{R}^+$, *and let*

$$LV(t, \xi) = V_t(t, \xi) + V_\xi(t, \xi)\, f(t, \xi) + \frac{1}{2} trace\,[g^T(t, \xi)\, V_{\xi\xi}(t, \xi)\, g(t, \xi)]. \tag{9}$$

We have ([**3**], [**5**])

1. *if*

$$LV(t, \xi) \leq 0 \tag{10}$$

for all $0 < |\xi| \leq k$, *then the trivial solution* $X_t \equiv 0$ *is* (*uniformly*) *stable in probability*;

2. *if*

$$LV(t, \xi) \leq -c(|\xi|)$$

where c *is a continuous, positive definite function on* $\mathbb{R}^+$, *then the trivial solution* $X_t \equiv 0$ *is asymptotically stable*;

3. *if* (10) *holds and*

$$\lim_{r \to +\infty} a(r) = \infty \tag{12}$$

then $X_t \equiv 0$ *is asymptotically stable in the large.*

Remark 1. *These results also hold if* g *is a* $n \times m$ *matrix valued function and* w_t *a* m*-dimensional Wiener process* ([**5**]).

Many problems concerning the stability of the equilibrium states of a nonlinear stochastic system can be reduced to problems concerning stability of solutions of the linear system obtained from the original system by dropping terms of higher than first order in ξ. Let $\overline{X}_t \equiv 0$ be a trivial solution of the n dimensional stochastic differential Ito equation (4). The linear generalized form of (4) is defined as follows

$$dX_t = F(t)\, X_t\, dt + G(t)\, X_t\, dw_t \tag{13}$$

where F and G are square n dimensional matrices, whose elements are

$$F_{i,j}(t, \overline{X}_t) = \frac{\partial f_i}{\partial x_j}(t, \overline{X}_t), \qquad G_{i,j}(t, \overline{X}_t) = \frac{\partial g_i}{\partial x_j}(t, \overline{X}_t)$$

$i, j = 1, \ldots, n$. Whenever $\overline{X}_t \neq 0$ is a stationary solution of (4), X_t in equation (13) has to be replaced by $X_t - \overline{X}_t$.

Theorem 2. *We have the following stability results* ([5]).

1. *If the trivial solution* $X_t \equiv 0$ *is asymptotically stable for the linear system* (13) *with constant coefficients* (*i.e.* $F(t) = F$ *and* $G(t) = G$) *and the coefficients of the system* (4) *satisfy the following inequality*

$$|f(t, \xi) - F\xi| + |g(t, \xi) - G\xi| < \gamma |\xi| \tag{14}$$

in a sufficiently small neighborhood of the position $\xi = 0$, *with a sufficiently small constant* γ, *then the trivial solution of* (4) *is asymptotically stable.*

2. *If for any* $x \neq 0$ *the solutions of the linear system* (13) *satisfy the identity*

$$\lim_{T \to +\infty} \sup_{s > 0} P\left(\inf_{\tau > s+T} |X_\tau(s, x)| < d \right) = 0 \tag{15}$$

for any $d > 0$, *and the elements of the matrices* F, G *are bounded, then the solution* $X_t \equiv 0$ *is unstable in probability for all systems* (4), *whose coefficients satisfy condition* (14), *with sufficiently small* γ.

3. *If the system* (13) *has constant coefficients, the assertion in* 2. *remains valid if assumption* (15) *is replaced by the requirement that for all* $x \neq 0$

$$P\left(\lim_{t \to +\infty} |X_t(s, x)| = +\infty \right) = 1 . \tag{16}$$

3 - The case study

We consider the stochastic differential equation system (3) which can be written as in (4) where

$$X_t = \begin{bmatrix} x_t \\ y_t \end{bmatrix}, \qquad f(t, X_t) = \begin{bmatrix} rx_t(1 - x_t) - q_0 x_t y_t \\ cq_0 x_t y_t - uy_t \end{bmatrix}, \qquad g(t, X_t) = \begin{bmatrix} -\sigma x_t y_t \\ c\sigma x_t y_t \end{bmatrix}$$

with r, c and u positive constants. It can be shown that the existence and uniqueness conditions of the solution hold.

From Definition 1, stationary solutions of (4) are, as for the deterministic case (1), the degenerate solutions $E_0 = (0, 0)$ and $E_1 = (1, 0)$. In order to study the stability of these stationary solutions, we consider the linear generalized form of (4) in $(\overline{x}, \overline{y})$ as defined in (13), where

$$F(\overline{x}, \overline{y}) = \begin{bmatrix} r(1-2\,\overline{x}) - q_0\overline{y} & -q_0\overline{x} \\ cq_0\overline{y} & cq_0\overline{x} - u \end{bmatrix}, \qquad G(\overline{x}, \overline{y}) = \begin{bmatrix} -\sigma\overline{y} & -\sigma\overline{x} \\ c\sigma\overline{y} & c\sigma\overline{x} \end{bmatrix}.$$

Theorem 3. *The stationary solution E_0 is always unstable for the system* (4).

Proof. The linearized problem in E_0 is the following deterministic dynamical system

$$\begin{cases} dx_t = rx_t\,dt \\ dy_t = -uy_t\,dt\,. \end{cases} \tag{17}$$

The instability of (17) follows immediately because the drift matrix $F(0, 0)$ has a positive eigenvalue $r > 0$. The solution of (17) corresponding to initial conditions $x_0 \neq 0$, $y_0 \neq 0$ at time $t = 0$, namely

$$\begin{cases} x_t = x_0\,e^{rt} \\ y_t = y_0\,e^{-ut} \end{cases}$$

is such that

$$\lim_{t \to +\infty} |X_t| = \lim_{t \to +\infty} (|x_t| + |y_t|) = +\infty \qquad a.s.$$

Moreover, the left hand side of (14) becomes

$$\sqrt{x^2(-rx - q_0 y)^2 + c^2 q_0^2 x^2 y^2} + \sqrt{x^2 y^2 \sigma^2 (c^2+1)}$$

which, in a small neighborhood of $(0, 0)$, say $]-\varepsilon, \varepsilon[\times]-\varepsilon, \varepsilon[$, is less than $\gamma|(x, y)|$ where γ is a constant going to zero as ε goes to zero. Therefore, being r and u constants, due to Theorem 2, the null solution is unstable for the original system (4). ■

Lemma 1. *If*

$$0 < q_0 < \frac{u}{c} - \frac{c\sigma^2}{2} \equiv T_1 \tag{18}$$

then the stationary solution E_1 *is an asymptotically stable solution of the linearized system*

$$\begin{cases} dx_t = (-r(x_t - 1) - q_0 y_t)\, dt - \sigma y_t\, dw_t \\ dy_t = (cq_0 - u)\, y_t\, dt + c\sigma y_t\, dw_t. \end{cases} \tag{19}$$

Proof. Consider the function

$$V(x, y) = (x-1)^2 + \frac{q_0^2 + 2r\sigma^2}{2r(2u - 2cq_0 - c^2\sigma^2)} y^2. \tag{20}$$

Under condition (18), $V(x, y)$ is a Lyapunov function and

$$LV = -2\left(\sqrt{r}(x-1) + \frac{q_0}{2\sqrt{r}} y\right)^2 < 0$$

for all $(x, y) \neq (1, 0)$. Moreover, taking

$$a(|(x-1, y)|) = \min\left(1, \frac{q_0^2 + 2r\sigma^2}{2r(2u - 2cq_0 - c^2\sigma^2)}\right) |(x-1, y)|$$

$$b(|(x-1, y)|) = \max\left(1, \frac{q_0^2 + 2r\sigma^2}{2r(2u - 2cq_0 - c^2\sigma^2)}\right) |(x-1, y)|$$

the assumptions of Theorem 1 are verified, so the stationary solution E_1 is asymptotically stable in the large. ■

The stability of the stationary solution E_1 for the non-linear system (4) follows by Theorem 2. In fact we have

Theorem 4. *If condition* (18) *is verified, then the stationary solution* E_1 *is asymptotically stable for the non-linear system* (4).

Proof. It suffices to prove condition (14) and then applying Theorem 2 and Lemma 1 we immediately obtain the thesis. The left hand side of (14) becomes

$$\sqrt{(1-x)^2[-r(1-x)+q_0 y]^2+c^2 q_0^2 y^2(1-x)^2}+\sqrt{\sigma^2 y^2(1-x)^2+c^2\sigma^2 y^2(1-x)^2}$$

and this quantity in $]1-\varepsilon, 1+\varepsilon[\times]-\varepsilon, \varepsilon[$ (a small neighborhood of $(1,0)$) is less than $\gamma|(x-1, y)|$ with $\gamma=\max(|q_0-r|\varepsilon, cq_0\varepsilon, \sigma\varepsilon, c\sigma\varepsilon)$. ■

We proved, by means of sufficient Lyapunov conditions, that the stationary solution E_1 is asymptotically stable for (19) if condition (18) is verified. In order to study the instability for E_1 and find the related condition, we state

Lemma 2. *The solution of system* (19), *for an initial condition* (x_0, y_0) *at time* $t=0$, *takes the form*

$$X_t=\begin{bmatrix}1+a_{11}(t)(x_0-1)+y_0 a_{12}(t)\\ y_0 a_{22}(t)\end{bmatrix} \tag{21}$$

where

$$a_{11}(t)=e^{-rt}$$

$$a_{22}(t)=e^{t\left(cq_0-u-\frac{1}{2}c^2\sigma^2+c\sigma\frac{w_t}{t}\right)}$$

$$a_{12}(t)=\frac{\left(-q_0+\dfrac{1}{2}c\sigma^2-\sigma\dfrac{w_t}{t}\right)\left(e^{t\left(cq_0-u-\frac{1}{2}c^2\sigma^2+c\sigma\frac{w_t}{t}\right)}-e^{-rt}\right)}{\left(cq_0-u-\dfrac{1}{2}c^2\sigma^2+c\sigma\dfrac{w_t}{t}+r\right)}.$$

Proof. For an initial condition (x_0, y_0) at time $t=0$, the solution to system (19) is ([7])

$$X_t=\begin{bmatrix}1\\0\end{bmatrix}+\exp\{Q(t)\}\begin{bmatrix}x_0-1\\ y_0\end{bmatrix} \tag{22}$$

where

$$Q(t) = \begin{bmatrix} -rt & \left(-q_0 + \frac{1}{2}c\sigma^2\right)t - \sigma w_t \\ 0 & \left(cq_0 - u - \frac{1}{2}c^2\sigma^2\right)t + c\sigma w_t \end{bmatrix}.$$

By the definition of exponential of operators ([4]):

$$\exp\{Q(t)\} = \sum_{n=0}^{\infty} \frac{1}{n!}[Q(t)]^n$$

$$= \begin{bmatrix} \sum_{n=0}^{\infty} \frac{1}{n!}(-rt)^n & \left[\left(-q_0 + \frac{1}{2}c\sigma^2\right)t - \sigma w_t\right] D(t) \\ 0 & \sum_{n=0}^{\infty} \frac{1}{n!}\left[\left(cq_0 - u - \frac{1}{2}c^2\sigma^2\right)t + c\sigma w_t\right]^n \end{bmatrix}$$

where

$$D(t) \equiv \sum_{n=0}^{\infty} \frac{1}{n!} \sum_{k=0}^{n-1} (-rt)^k \left[\left(cq_0 - u - \frac{1}{2}c^2\sigma^2\right)t + c\sigma w_t\right]^{n-1-k}.$$

Direct calculation leads to

$$D(t) = \frac{e^{\left(cq_0 - u - \frac{1}{2}c^2\sigma^2\right)t + c\sigma w_t} - e^{-rt}}{\left(cq_0 - u - \frac{1}{2}c^2\sigma^2 + r\right)t + c\sigma w_t}.$$

Then, it follows that

$$\exp\{Q(t)\} = \begin{bmatrix} a_{11}(t) & a_{12}(t) \\ 0 & a_{22}(t) \end{bmatrix}$$

and from (22) we immediately obtain (21). ■

The availability of the solution of (19) allows us to determine instability conditions of the stationary solution E_1 by studying its asymptotical behaviour. In fact, it holds

Theorem 5. *If*

$$q_0 > \frac{u}{c} + \frac{1}{2} c\sigma^2 \equiv T_2 \tag{23}$$

then the stationary solution E_1 *is unstable for the original system* (4).

Proof. We note that

$$\left| \begin{bmatrix} x_t - 1 \\ y_t \end{bmatrix} \right| = \sqrt{[a_{11}(t)(x_0 - 1) + y_0 a_{12}(t)]^2 + y_0^2 a_{22}^2(t)}$$

and

$$\lim_{t \to +\infty} a_{11}(t) = 0 \,.$$

Moreover, under condition (23),

$$\lim_{t \to +\infty} a_{22}^2(t) = +\infty \qquad \lim_{t \to +\infty} a_{12}^2(t) = +\infty \,.$$

It follows that the assumptions of Theorem 2 are verified (condition (14) holds - see the proof of Theorem 4) and the stationary solution E_1 is unstable for the system (4), under condition (23). ■

Remark 2. *We have obtained that the stationary solution* E_0 *is always unstable while the stationary solution* E_1 *is asymptotically stable when condition* (18) *holds and unstable under condition* (23). *For* $T_1 < q_0 < T_2$ *we have not obtained a stability result for* E_1; *however, from numerical simulations, it appears that it is still stable.*

4 - Numerical simulations and concluding remarks

Previous results about the stability of E_1 under condition (18) and the instability under condition (23) are confirmed by numerical simulations (Figure 1).

We have assumed ([**1**])

$$r = 0.1971 \qquad u = 0.1913 \qquad c = 0.1991 \,.$$

In such a case the threshold value in (23) for $\sigma = 1$ is $T_2 = 1.0602$ while the value T_1 in (18) is $T_1 = 0.8611$.

If condition (23) is verified E_1 is unstable and the solution of system (4) fluctuates around the deterministic equilibrium E^* (Figure 2). This suggests that, in

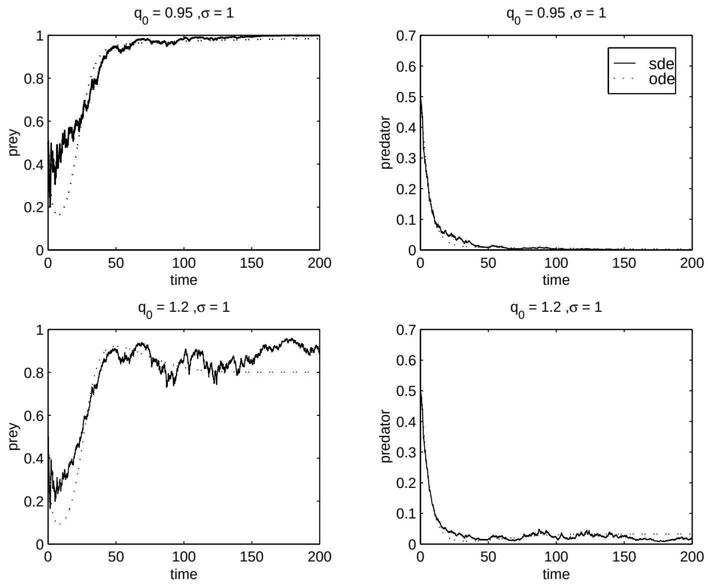

Figure 1 - Deterministic and stochastic trajectories of prey and predator for initial conditions $x_0 = 0.5$, $y_0 = 0.5$. Time is in days.

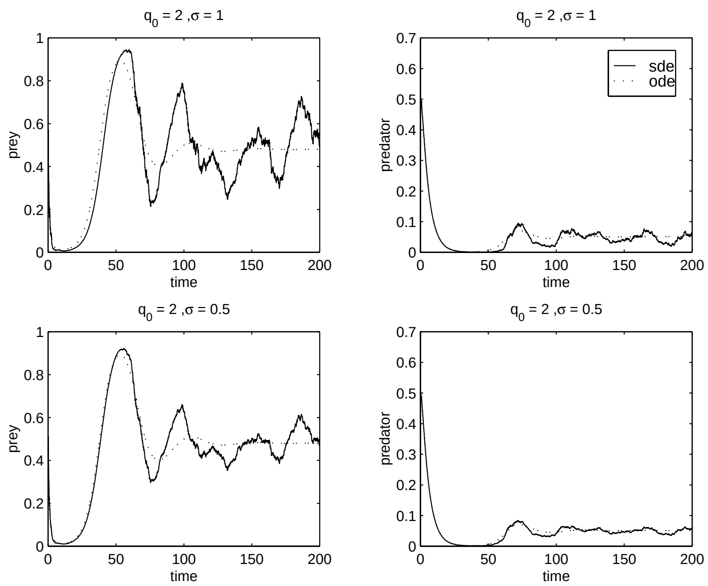

Figure 2 - Deterministic and stochastic trajectories of prey and predator for initial conditions $x_0 = 0.5$, $y_0 = 0.5$ for different values of σ. Time is in days.

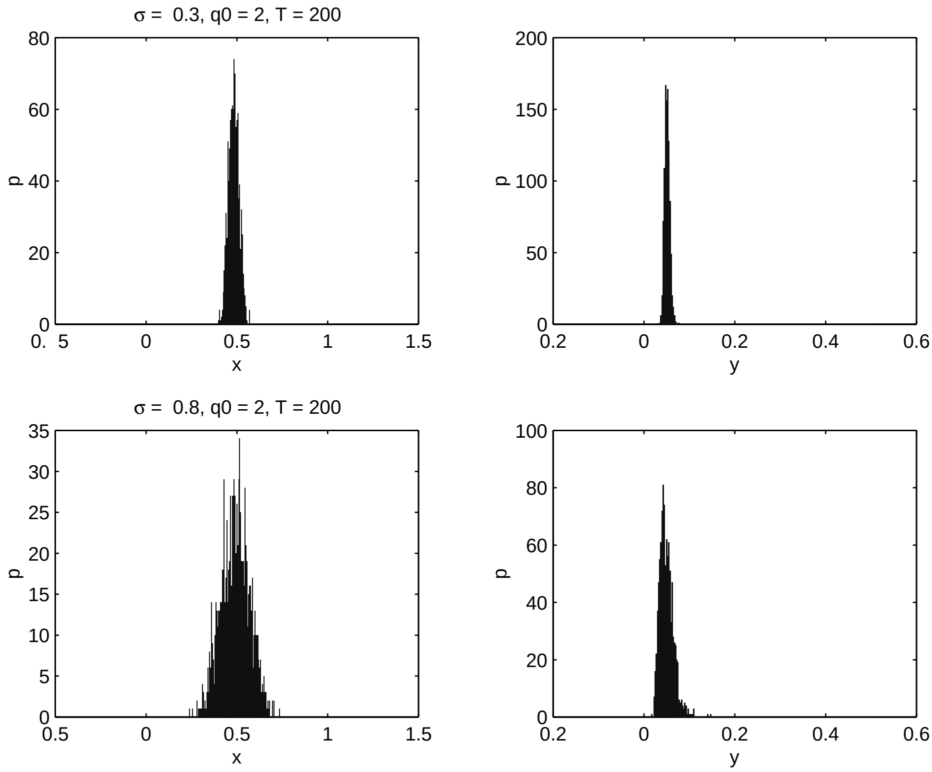

Figure 3 - Histogram for the distribution of the solution of the system (2.6) for T=200 days.

the stochastic case, there is a solution whose distribution is the stochastic analogous of the deterministic stationary solution E^*.

We observe that associated to the states $E_0 = (0, 0)$ and $E_1 = (1, 0)$ there are Dirac delta distributions and we can ask if there exists a further invariant distribution.

The density of such a distribution is an equilibrium solution of the Fokker-Plank equation

$$\begin{aligned} &\frac{\partial}{\partial x}[(rx(1-x) - q_0 xy)\, p(x, y)] + \frac{\partial}{\partial y}[(cq_0 xy - uy)\, p(x, y)] \\ (24) \quad &= \frac{1}{2}\left\{ \frac{\partial^2}{\partial x^2}[\sigma^2 x^2 y^2 p(x,y)] + 2\,\frac{\partial^2}{\partial x\,\partial y}[-c\sigma^2 x^2 y^2 p(x,y)] + \frac{\partial^2}{\partial y^2}[c^2\sigma^2 x^2 y^2 p(x,y)] \right\} \end{aligned}$$

for $(x, y) \in D$ where D is an open set in $\mathbb{R}^2$ containing the support of $p(x, y)$.

This equation is not simple to solve. To see if there is a further invariant distribution, solution of (24), besides the Dirac distributions, we simulated 1000 trajectories of the solution of system (4) for $q_0 = 2$. Then we plotted histograms for 1000 values (x_t, y_t) with $t = 200$ (Figure 3).

As we can see, the simulated values (x_{200}, y_{200}) are distributed around the deterministic equilibrium $E^* = (0.4803, 0.0512)$ and, as σ decreases, the values of (x_{200}, y_{200}) approach E^*.

In this work we propose only numerical results of equation (24) which is still in study, but previous histograms suggest the existence of an invariant distribution corresponding to a process which could be the stochastic analogous of the deterministic equilibrium E^*.

From the biological point of view, the introduction of a noise in the deterministic differential equation (1) modifies the deterministic stability threshold $\frac{u}{c}$ of the equilibrium solution E_1 giving rise to new thresholds. If the variability of predator search efficiency q_0 is large, the stability threshold can be seriously modified in respect to the deterministic one. The results show that there are two thresholds T_1 and T_2 for q_0, depending on σ: T_1 under which E_1 is asymptotically stable and T_2 over which E_1 is unstable, but numerical simulations show that the stability threshold could be equal to T_2. In fact stability for E_1, when $q_0 < T_1$, was proved by means of a sufficient Lyapunov condition. A direct prove will probably need to verify if the equilibrium solution E_1 satisfies Definition 2 when condition (23) holds.

A further problem is to show the existence of an invariant distribution and determine its density as solution of the Fokker-Plank equation. The study of such problems is still in progress together with that one of estimating q_0 in (3) starting from samples from the two populations.

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Abstract

In this paper we study the stability of equilibrium solutions of a stochastic differential equation derived by a Lotka-Volterra predator-prey model by introducing a noise on a parameter.

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