A stochastic model for predator-prey systems: basic properties, stability and computer simulation

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Abstract. A simple stochastic description of a model of a predator-prey system is given. The evolution of the system is described by means of Itô's stochastic differential equations (SDEs), which are the natural stochastic generalization of the Lotka–Volterra deterministic differential equations. Since these SDEs do not satisfy the usual conditions for the existence and uniqueness of the solution, we state a theorem of existence; moreover we study the stability of the equilibrium point and perform a computer simulation to study the behaviour of the trajectories of solutions with given initial data and to estimate first and second moments.

1. Introduction

In this paper, we deal with a simple stochastic version of a predator-prey system. This system belongs to a wide class of two-dimensional stochastic models obtained as an extension of the well-known Lotka–Volterra model; these models have received much attention both in the deterministic and stochastic case (see, for instance [4, 10, 14, 20, 22, 23]), since they are able to describe interacting populations, chemical reactions, genetic evolution, and many other phenomena in the life sciences.

It is well known (see, e.g., [9, 17, 19]) that the need for randomizing classical deterministic equations and thus considering stochastic models is related to the presence of random environmental fluctuations (external randomness) and/or to the effect of internal randomness (due to random fluctuations in growth, generations and deaths of individuals into the population) known as demographic stochasticity.

In many classical works, recurrence properties, stability, existence of the equilibrium probability distribution, and extinction probabilities for stochastic models of interacting populations are considered, with regard to random environmental fluctuations or to noise perturbations of parameters. Indeed, one supposes that some parameter α (such as the carrying capacity, or a competition

coefficient, or intrinsic growth rate) varies randomly according to the equation $\alpha = \alpha_0 + \Lambda(t)$, where α_0 is a constant, being the mean value of α, and $\Lambda(t)$ represents a white noise with mean zero and a certain variance σ^2 (see, e.g., [11, 22, 24]).

The external (environmental) randomness leads to destabilizing effects and to extinction of the population under certain conditions [11, 22].

In this paper we consider internal randomness. By modelling the process by means of stochastic differential equations we are able to prove the existence of the solution of these equations for all time, and the impossibility of extinction.

At this point, it is appropriate to consider the mean of the stochastic differential equation, that is in what sense one has to interpret the stochastic differential of a process X_t.

At least, two possible definitions of stochastic differential are available, which lead, respectively, to Itô's calculus and Stratonovich's calculus. Many authors have considered which of the two approaches is more suitable in any particular circumstance (see, e.g., [25]). For instance, in the case of environmental randomness, Ricciardi has pointed out that Stratonovich's and Itô's differential equations related to given difference equations describe two different dynamical systems, with the first arising when the intrinsic continuity of the process is assumed, the latter when this condition does not hold [25].

In our model, since we consider internal randomness, a description of the evolution of populations by means of birth and death processes is more appropriate (similar models have been proposed earlier, e.g., in [6, 15]). This leads to a description in terms of martingales. Indeed, the above considerations ultimately suggest that we formulate the evolution of the system by means of Itô's stochastic differential equations (SDE's). These SDEs do not satisfy the usual conditions for the existence and uniqueness of the solution; so, we shall deal with a theorem of existence of the solution for all time.

Although other authors have studied systems of stochastic differential equations under a variety of "non usual" conditions on the coefficients (see, e.g., [18]), our results appear to be new.

From the existence theorem, it also follows that the extinction probability for both populations is zero. This is not surprising, if we compare it with other results in the classical literature [22] in which external randomness is considered, and the population is soon extinguished if the intensity of random fluctuations is too large. Indeed, in our model, if we denote the deterministic component by u, the stochastic perturbation is of order $u^{1/2}$, as internal fluctuations are represented.

We assume a Gompertz growth model for prey; one should recall that, in the case of a population following the Gompertz law, if external randomness is considered (such as random fluctuations of the population's carrying capacity), one can prove that persistence of the population in the environment is independent of the intensity of the environmental fluctuations [21].

Besides dealing with the existence of the solution, we study the stochastic stability of the system of stochastic differential equations obtained, and we simulate by means of a computer, the trajectories of the solutions with given initial data; so we can consider the effects due to internal randomness of the model.

Numerical simulations allow us to study the behaviour of the solution as a function of time, with regard to the stochastic stability of the nontrivial equilibrium point. Many simulation runs are carried out to estimate the first and second moment of solutions.

In Sect. 2 we deal with the mathematical framework for the biological model which is described by means of a system of Itô's stochastic differential equations. To make their meaning more transparent, we start with a birth-and-death-like model and show our stochastic differential equations follow naturally from it.

In Sect. 3 we study stability and in Sect. 4. we state a theorem of existence, for the solution of the system of SDEs considered. Section 5 is finally devoted to numerical simulation.

2. Mathematical description of the biological model

First, let us consider a population of prey in the absence of predators. The time evolution of such a population can be described in terms of "birth-and-death" processes. Indeed, let $X(t)$ be the number of prey individuals at time t, where $X(t)$ is a random variable (r.v.), since its values depend on many random factors.

Let us consider now a single individual of the prey population. If $\Delta_0 X(t)$ is the increment of the r.v. $X(t)$ during the time interval $(t, t + \Delta t)$, due to the individual considered, $\Delta_0 X(t)$ is also a r.v. which can take the values $\pm 1, 0$ corresponding, respectively, to the birth of a new prey, the death of the considered prey, and the case in which it merely remains alive, during the time interval $(t, t + \Delta t)$.

More generally, we can speak of "growth" of prey, rather than "birth"; if the prey population is very simple (e.g., unicellular organisms) growth simply means birth of a new individual. For more complex populations, we may have to wait some convenient time δ for the generation and birth of a new individual.

We can suppose that we are in the case of *nonoverlapping events*, i.e. during the time interval $(t, t + \Delta t)$ one and only one of the above mentioned events can occur.

So, if we consider a time interval of length dt, we have

$$P(d_0 X(t) = +1/F_t) = \lambda_1(t) \, dt$$
$$P(d_0 X(t) = -1/F_t) = \mu_1(t) \, dt + \varphi(X(t)) \, dt \qquad (2.1)$$
$$P(d_0 X(t) = 0/F_t) = 1 - [\lambda_1(t) + \mu_1(t) + \varphi(X(t))] \, dt,$$

where $d_0 X(t)$ represents the increment of the population due to the single individual considered over the interval of length dt, $P(-/-)$ is the conditional probabilty that the r.v. $X(t)$ has an increment $d_0 X(t)$ over $(t, t + dt)$, given all events until the time t, and F_t denotes the σ-algebra of the *past* (i.e. F_t is the σ-algebra generated by $\{X(s), 0 \leqslant s \leqslant t\}$).

The quantity $\lambda_1(t)$ is the growth rate of prey, $\mu_1(t)$ is the death rate of prey; the term $\varphi(X(t))$ introduces a further death rate due to the boundedness of disposable food resources (this term is typically proportional to $X(t)$).

The parameters in Eqs. (2.1) are called the *intensities* of the process, as a natural generalization of the Poisson process. If we consider not only a single prey, but the whole population, all the right members of Eqs. (2.1) have to be multiplied by $X(t)$ and we obtain

$$P(dX(t) = +1/F_t) = P(d_0 X(t) = 1/F_t) X(t)$$
$$P(dX(t) = -1/F_t) = P(d_0 X(t) = -1/F_t) X(t) \qquad (2.2)$$
$$P(dX(t) = 0/F_t) = 1 - [P(dX(t) = +1/F_t) + P(dX(t) = -1/F_t)],$$

where $dX(t)$ represents the increment of the whole prey population over the interval $(t, t + dt)$.

So, from (2.2) we obtain the conditional expectation, that from now on we shall assume as positive, for the increment $dX(t)$

$$E(dX(t)/F_t) = [\lambda_1(t)\, dt - \{\mu_1(t) + \varphi(X(t))\}\, dt]X(t) > 0. \tag{2.3}$$

If we define a process $M_0(t)$ (with $M_0(0) = 0$) as having increments

$$dM_0(t) = dX(t) - E(dX(t)/F_t), \tag{2.4}$$

then

$$E(dM_0(t)/F_t) = 0, \tag{2.5}$$

that is the process

$$M_0(t) = X(t) - \int_0^t [\lambda_1(s) - \{\mu_1(s) + \varphi(X(s))\}]X(s)\, ds \tag{2.6}$$

is a martingale.

The equation (2.5) is the Doob–Meyer decomposition of the sub-martingale $X(t)$. The process $X(t)$ is a counting process and the equation

$$X(t) = \Theta(t) + M_0(t) \equiv \int [\lambda_1(s) - \{\mu_1(s) + \varphi(X(s))\}]X(s)\, ds + M_0(t) \tag{2.7}$$

gives the process $X(t)$ as a function of the intensity $\theta(t) = [\lambda_1(t) - \{\mu_1(t) + \varphi(X(t))\}]X(t)$ and of a random noise component (the martingale $M_0(t)$).

The conditional variance of the increments of the martingale $M_0(t)$ is given by (see, e.g., [1] or [2])

$$\mathrm{Var}(dM_0(t)/F_t) = \mathrm{Var}\{dX(t) - [\lambda_1(t)\, dt - (\mu_1(t) + \varphi(X(t)))\, dt]X(t)/F_t\}$$
$$= \mathrm{Var}(dX(t)/F_t), \tag{2.8}$$

since $\lambda_1(t)$, $\mu_1(t)$, $\varphi(X(t))$ are predictable, i.e. fixed for given F_t, and $X(t)$ is F_t-measurable.

Because $dX(t)$ is a variable taking on values $\pm 1, 0$ with conditional expectation given by (2.3), we find

$$\mathrm{Var}(dM_0(t)/F_t) = [\lambda_1(t) + \mu_1(t) + \varphi(X(t))]X(t)\, dt - [\lambda_1(t) + \mu_1(t)$$
$$+ \varphi(X(t))]^2 X(t)^2\, dt^2 \approx [\lambda_1(t) + \mu_1(t) + \varphi(X(t))]X(t)\, dt \tag{2.9}$$

up to a first order approximation in dt.

Remark 2.1. Although $M_0(t)$ is not a continuous process, we assume the possibility of "approximating" the martingale $M_0(t)$ by a continuous Gaussian martingale $W(t)$, i.e. a Wiener process whose increments have expectation zero and variance given by the conditional variance of the increment of the martingale $M_0(t)$ (see (2.9)). Heuristically, this fact follows by an argument of the central limit theorem for martingales [7, 8].

Until this moment, we have supposed that predators were absent. If the predator population is present within the same habitat, we have to modify Eq. (2.7). Indeed, we must consider a new additional death rate $\gamma_1(t)$ for the prey population, that is $\gamma_1(t)\, dt$ represents the conditional probability that a prey is

killed by an individual predator, during a time interval of length dt. So, the 2nd line of (2.2) becomes

$$P(dX(t) = -1/F_t) = \{\mu_1(t)dt + \gamma_1(t)Y(t)dt + \varphi(X(t))\,dt\}X(t), \qquad (2.10)$$

where $Y(t)$ is the number of predators that are present at time t in the common habitat. Then, the time evolution of the prey population is described by the equation

$$X(t) = \tilde{\Theta}(t) + M(t) \equiv \int [\lambda_1(s) - \mu_1(s) - \gamma_1(s)Y(s) - \varphi(X(s))]X(s)\,ds + M_1(t),$$

$$(2.11)$$

where $M_1(t)$ is the martingale such that

$$dM_1(t) = dX(t) - E(dX(t)/F_t), \qquad E(dM_1(t)/F_t) = 0, \qquad (2.12)$$

with $E(dX(t)/F_t)$ given by (2.3) plus the term $-\gamma_1(t)X(t)Y(t)\,dt$, and whose increments have the approximate conditional variance given by (see (2.9))

$$\text{Var}(dM_1(t)/F_t) \approx [\lambda_1(t) + \mu_1(t) + \gamma_1(t)Y(t) + \varphi(X(t))]X(t)\,dt. \qquad (2.13)$$

Analogously, for the predator population, we have

$$P(dY(t) = +1/G_t) = [\lambda_2(t) + \beta\gamma_1(t)X(t)]Y(t)\,dt$$
$$P(dY(t) = -1/G_t) = \mu_2(t)Y(t)\,dt \qquad (2.14)$$
$$P(dY(t) = 0/G_t) = 1 - \{[\lambda_2(t) + \beta\gamma_1(t)X(t)]Y(t) - \mu_2(t)Y(t)\}\,dt,$$

where $dY(t)$ represents the increment of the entire predator population over the time interval of length dt, $P(\text{-}/\text{-})$ is the conditional probability that the r.v. $Y(t)$ ($\#$ of predators at time t) has an increment $dY(t)$ over $(t, t + dt)$, with respect to the σ-algebra of the "past" G_t (G_t is the σ-algebra generated by $\{Y(s), s \leqslant t\}$).

The term $\lambda_2(t)$ is the (natural) growth rate of predators (i.e. in the absence of prey); $\mu_2(t)$ is the (natural) death rate; β is the biomass conversion constant, that is $\beta\gamma_1(t) \doteq \gamma_2$ is the growth rate of a single predator on having killed a prey.

As for the prey population, we can write $Y(t)$ in terms of a deterministic part (see (2.4)) and a random part, the martingale $M_2(t)$ whose increments have conditional expectation zero and conditional variance given by

$$\text{Var}(dM_2(t)/G_t) \approx [\lambda_2(t) + \beta\gamma_1(t)X(t) + \mu_2(t)]Y(t)\,dt \qquad (2.15)$$

up to a first order approximation in dt. Therefore, we obtain the following system of stochastic differential equations for the variables $X(t)$, $Y(t)$:

$$dX(t) = X(t)\{(\lambda_1 - \mu_1 - \gamma_1 Y(t) - \varphi(X(t))\,dt\} + dM_1(t)$$
$$dY(t) = Y(t)\{(\lambda_2 + \beta\gamma_1 X(t) - \mu_2)\,dt\} + dM_2(t), \qquad (2.16)$$

where, for simplicity, we have omitted the dependence of the parameters on their arguments.

Typically, the values of the parameters in the Eq. (2.16) for a predator-prey system are such that

$$\mu_1 \ll \gamma_1 (\text{much smaller than}); \qquad \gamma_1 < \lambda_1$$
$$\lambda_2 \ll \gamma_2, \quad \mu_2 \ll \gamma_2; \qquad \varphi(X) \ll \gamma_1 \text{ for small } X.$$

Then, in a simplified model, μ_1 (death rate of prey in absence of predators) and λ_2 (birth rate of predator in the absence of prey) may be neglected.

If we replace the martingales M_t^1, M_t^2 in Eqs. (2.16), respectively, with the products of independent standard Brownian motions W_t^1, W_t^2 times the square root of the conditional variances of dM_t^1 (see Remark 2.1), and we introduce the above simplifications, Eqs. (2.16) become

$$dX_t = X_t(\lambda_1 - \gamma_1 Y_t - \varphi(X_t))\, dt + [X_t(\lambda_1 + \gamma_1 Y_t + \varphi(X_t))]^{1/2}\, dW_t^1$$
$$dY_t = Y_t(-\mu_2 + \gamma_2 X_t)\, dt + [Y_t(\mu_2 + \gamma_2 X_t)]^{1/2}\, dW_t^2. \tag{2.17}$$

Instead of (2.17) one may study the more general system:

$$dx = (xq(x) - yp(x))\, dt + [x|q(x)| + yp(x)]^{1/2}\, dW_t^1$$
$$dy = y(-s + cp(x))\, dt + [y(s + cp(x)]^{1/2}\, dW_t^2. \tag{2.18}$$

Here, $q(x)$ is the specific growth rate of the prey; $p(x)$ is the predator functional response, s is the predator specific death rate; c is the biomass conversion constant. The functions $p(x)$, $q(x)$ are supposed to satisfy the following properties:

$$q(x(0)) = \alpha > 0; \quad q'(x) \leqslant 0 \quad \text{and} \quad \exists K > 0 \text{ s.t. } q(K) = 0$$
$$p(0) = 0; \quad p'(x) > 0, \tag{2.19}$$

K is the carrying capacity of the environment.

The system (2.18) with conditions (2.19) is reduced to (2.17) with the choices:

$$s = \mu_2$$
$$p(x) = \gamma_1 x$$
$$\gamma_2 x = cp(x); \qquad 0 < c = \gamma_2/\gamma_1 \leqslant 1 \tag{2.20}$$
$$q(x) = \lambda_1 - \varphi(x).$$

There are many acceptable forms for the function $q(x)$; the simplest is the density independent growth rate, that is $q(x) = \lambda = $ constant (this corresponds to unbounded exponential growth, $\varphi(x) = 0$).

Among density-dependent growth rates we can consider

$$q_1(x) = \lambda(1 - x/k) \quad \text{or} \quad q_2(x) = \lambda b_0 \cdot \ln(k/x). \tag{2.21}$$

If $b_0 \approx [\ln(k/x(0))]^{-1}$, we have $q_2(x) \approx \lambda$ for x close to $x(0)$ and so we have exponential growth for small x; globally, the deterministic equation $\dot{x} = xq_2(x)$ describes the so-called "Gompertz law". That is, its solution with initial value $x(0)$ is

$$x(t) = x(0) \exp[\ln(k/x(0)) - (1 - \exp(-\lambda b_0 t)],$$

whose graph is a sigmoid curve that approaches k as t gets large; k is the value saturation.

The Gompertz law seems to describe well enough the deterministic growth of simple populations (as prey in the absence of predators). However, we observe that the Gompertz law can be "approximated" as closely as desired with the Logistic law by a proper choice of the parameters (see, e.g., [9]).

Since the function $xq_2(x)$ has an infinite derivative at $x = 0$, we consider a more regular smoothing $\psi(x)$ of $xq_2(x)$ near $x = 0$, that is $\psi(x)$ is a C^2 function defined for $x \geqslant 0$ which has bounded derivatives and is a "little" different from $xq_2(x)$ only for small $x \geqslant 0$. In the sequel, we choose

$$q(x) = x^{-1}\psi(x) \tag{2.22}$$

in Eqs. (2.18). This is only a technical condition to ensure that all the coefficients of the equations are Lipschitz continuous, near $x = 0$.

Our system will be written:

$$
\begin{aligned}
dx &= (xq(x) - \gamma xy)\, dt + [x|q(x)| + \gamma xy]^{1/2}\, dW_t^i \\
dy &= y(-s + c\gamma x)\, dt + [y(s + c\gamma x)]^{1/2}\, dW_t^2,
\end{aligned}
\tag{2.23}
$$

where $q(x)$ is given by (2.22). The Itô stochastic differential equations (2.23) represent a suitable manner of describing a stochastic model for the system of interacting populations submitted to internal randomness; here, the fluctuations which depend on the occurrences of births and deaths are of Poisson type.

3. Stability for the system (2.23)

In this section we deal with stability for the system of stochastic differential equations (2.23) describing our physical model of predator-prey interaction. For the moment, we do not consider any question of existence and uniqueness of the solution with given initial data; this problem will be treated in Sect. 4. Here, we examine the equilibrium points for the deterministic part of Eq. (2.23) (drift-equilibrium points) that is

$$
\begin{aligned}
\dot{x} &= xq(x) - \gamma xy \\
\dot{y} &= y(-s + c\gamma x),
\end{aligned}
\tag{3.1}
$$

where $q(x)$ is given by (2.22).

The equilibrium points for (3.1) are given by the solutions of

$$
\begin{aligned}
xq(x) - \gamma xy &= 0 \\
y(-s + c\gamma x) &= 0.
\end{aligned}
\tag{3.2}
$$

We find the trivial equilibrium point $(x, y) = (0, 0)$ and the nontrivial one (3.3) $(x^*, y^*) = (s/c\gamma, (1/\gamma) \cdot q(s/c\gamma))$.

By means of well-known techniques (see, e.g., [22]), it easily follows that the equilibrium point given by (3.2) is asymptotically stable for the deterministic part of (2.23). Therefore, we have stability of the expectation values of x_t, y_t in Eqs. (2.23) that is the drift equilibrium point (x^*, y^*) is stable in mean for Eqs. (2.23). In fact, as we shall see in Sect. 5, numerical simulations show that (x^*, y^*) is also stochastically stable for the system (2.23).

4. Existence of the solution with given initial data

We rewrite Eqs. (2.18) with initial values x_0, y_0:

$$
\begin{aligned}
dx_t &= (x_t q(x_t) - p(x_t)y_t)\, dt + (x_t|q(x_t)| + p(x_t)y_t)^{1/2}\, dW_t^1 \\
dy_t &= y_t(-s + cp(x_t))\, dt + (y_t(s + cp(x_t)))^{1/2}\, dW_t^2 \\
x(0) &= x_0, \qquad y(0) = y_0
\end{aligned}
\tag{4.1}
$$

The function $q(x)$ is given by (2.22). Here, if u_i $(i = 1, 2)$ represent the deterministic terms (drift terms), the random perturbations (diffusion terms) are of order $u_t^{1/2}$, W_t^i being standard Brownian processes which we can assume to be indepen-

dent; the diffusion terms

$$\sigma_1(x, y) = (x|q(x)| + p(x)t)^{1/2}, \qquad \sigma_2(x, y) = (y(s + cp(x)))^{1/2} \qquad (4.2)$$

vanishes at zero population level.

As reported in the Introduction, the situation is quite different in other instances discussed in the classical literature where external (environmental) randomness is considered, and the random perturbation is of the same order as the deterministic term [22, 24].

Intuitively, one expects that the solution of the stochastic system (4.1) exists for all time and this solution is far from zero for non zero initial values. Mathematically, these facts are not trivial to prove; indeed, Eqs. (4.1) do not satisfy the usual growth conditions for global existence and uniqueness of the solutions (see, e.g., [3] or [13]), unfortunately.

In order to prove the existence of the solution with given initial data for all $t \geqslant 0$, we need to impose some technical conditions. Substantially, it would be enough to suppose that the diffusion terms behave like $\|(x, y)\|$, for $x, y \to 0$. We fix a small $r > 0$ once for all and suppose that:

(C1) the function $xq(x)$ in (4.1) is replaced with another function $\tilde{Q}(x)$ such that $\tilde{Q}(x)$ is a "flattening" of $xq(x)$ around $x = 0$, in the following sense: $\tilde{Q}(x)$ is a C^2 function defined for $x \geqslant 0$ which behaves like const$(r)x^2$ for $0 \leqslant x \leqslant r$, it is joined by a smooth function for $r < x < 2r$ and $\tilde{Q}(x) = xq(x)$ for $x \geqslant 2r$; moreover $\tilde{Q}(x)$ has bounded derivatives.

(C2) the function $p(x)$ in (4.1) is a C^2 function defined for $x \geqslant 0$ having bounded derivatives such that $p(x)$ behaves like const$(r)x^2$ for $0 \leqslant x \leqslant r$ and $p(x) = \gamma x$ for $x \geqslant 2r$.

(C3) the quantities sy and cy in (4.1) are replaced, respectively with positive C^2 functions $c(y)$ and $s(y)$ defined for $y \geqslant 0$, having bounded derivatives, such that they behave like const$(r)y^2$ for $0 \leqslant y \leqslant r$ and $c(y) = cy$, $s(y) = sy$ for $y \geqslant 2r$.

If we take r and choose appropriately the joining functions between r and $2r$, the above functions are a sort of "regularized approximation" of the original functions in (4.1), in the sense, that for values of the arguments smaller than $2r$, there are some "little" differences (of course, this does not mean those differences became arbitrarily uniformly "small" for $r \to 0$!). In practice, if r is chosen small enough, any function f depending on a physical variable $u > 0$ can be "approximated" near $u = 0$ as in the construction above, without changing the behaviour of f for significant values of u (i.e. u large enough).

Thanks to conditions (C1), (C2), (C3) we can avoid some technical difficulties in the mathematical proof of the existence of the solution of the stochastic differential equations with given initial data. Thus, in the following, we assume a small $r > 0$ has been fixed once for all and we will consider the system:

$$dx = [\tilde{Q}(x) - p(x)y] \, dt + [|\tilde{Q}(x)| + p(x)y]^{1/2} \, dW_t^1$$

$$dy = [-s(y) + c(y)p(x)] \, dt + [s(y) + c(y)p(x)]^{1/2} \, dW_t^2 \qquad (4.3)$$

$$x(0) = x_0, \qquad y(0) = y_0.$$

We remark that, if $r > 0$ is small enough, the solution of (4.3) starting from positive, large enough values, evolves in accordance with system (2.23), if the solution remains far enough from zero. Moreover, the non trivial drift-equi-

librium point of (4.3) which is significant from a biological point of view (that is for $x, y \geqslant 1$), coincides with (x^*, y^*) given by (3.2), if r is small enough.

Now, we introduce the infinitesimal generator for Eq. (4.3), which is defined, for a C^2 function $f(x, y)$, by

$$
\begin{aligned}
Lf(x, y) = {} & \left\{ [\tilde{Q} - p(x)y] \frac{\partial f}{\partial x} + [-s(y) + c(y)p(x)] \frac{\partial f}{\partial y} \right\} \\
& + \frac{1}{2} \left\{ [|\tilde{Q}(x)| + p(x)y] \frac{\partial^2 f}{\partial x^2} + [s(y) + c(y)p(x)] \frac{\partial^2 f}{\partial y^2} \right\} \\
= {} & L^0 f(x, y) + L^1 f(x, y).
\end{aligned}
\tag{4.4}
$$

Here L^0 is the differential operator defined by the $\{\ \}$ and it corresponds to the deterministic part of Eq. (4.3), while the other part, L^1 refers to the random part.

We consider the nonnegative function defined for $(x, y) \in R^+ \times R^+$:

$$
V(x, y) = (x - x^*) - x^* \ln(x/x^*) + (y - y^*) - y^* \ln(y/y^*).
\tag{4.5}
$$

As it is easy to see, we have

$$
\begin{aligned}
LV(x, y) = {} & \left[\tilde{Q}(x) - p(x)y \right] \left(\frac{x - x^*}{x} \right) + \left[(-s(y) + c(y)p(x)) \left(\frac{y - y^*}{y} \right) \right] \\
& + \frac{1}{2} \left[\frac{x^*}{x^2} (|\tilde{Q}(x)| + yp(x)) + \frac{y^*}{y^2} (s(y) + c(y)p(x)) \right].
\end{aligned}
\tag{4.6}
$$

Now we recall the following result due to the Khas'minskij [16]:

Theorem 4.1. *Let $\{K_n\}_{n \in N}$ be an increasing sequence of compact set such that $\bigcup_{n \in N} K_n = \Omega$, where Ω is an open set of R^d. Let us consider the system:*

$$
dx = a(t, x) \, dt + \sigma(t, x) \, dW,
\tag{4.7}
$$

where W is a d-dimensional Wiener process with independent components and the coefficients $a(t, x)$, $\sigma(t, x)$ are Lipschitz continuous and bounded in each set $R^+ \times K_n$; let $V: R^+ \times \Omega \to R$ be a function that is C^1 in $t \in R^+$ and C^2 in $x \in \Omega$ such that
(i) $\exists \alpha > 0$ s.t. $LV \leqslant \alpha V$;
(ii) $\inf_{t > 0, x \in \Omega \setminus Kn} V(t, x) \to \infty$ for $n \to \infty$.
Assume for (4.7) the initial condition $x(0)$ which is independent of the process $W(t) - W(0)$ and such that $P\{x(0) \in \Omega\} = 1$.

Then there is a unique (up to equivalence) solution $x(t)$, $0 \leqslant t \leqslant T$, $\forall T > 0$, to the above mentioned initial value problem such that
(a) $x(t)$ is a diffusion process, homogeneous in time if a and σ are independent of t in (4.7);
(b) $P\{x(t) \in \Omega\} = 1$, $\forall t \geqslant 0$. □

Indeed, in order to prove the above result with $\Omega = (0, +\infty)^2$ it is enough to show the following facts (for more details, see [16]):

(i) A local solution $(x(t), y(t))$ exists because the coefficients of the equation are Lipschitz continuous and bounded in any bounded set. Moreover, the local solution with given initial data can be extended for all time $t \geqslant 0$; this is equivalent to saying that "explosions" are impossible, that is, if τ_∞ is the first exit time of the solution from every bounded domain, or briefly the escape time

to infinity, the following equality holds:

$$P(\tau_\infty = \infty) = 1. \tag{4.8}$$

(ii) Any solution starting from positive initial values does not leave the set $(0, +\infty) \times (0, +\infty)$, that is, if $\tau_0 = \inf\{t \geq 0 : x(t) = 0 \text{ or } y(t) = 0\}$ (the first time in which the solution reaches the x or y axis), one has

$$P(\tau_0 = \infty) = 1. \tag{4.9}$$

Indeed, since the biological model is discrete, the extinction of a population cannot be seen as the passage to zero, but it should be defined, for instance, as the reaching of a level at which the population no longer reproduces. However, in the continuous approximation, for extinction we simply mean population zero.

If $W(x, y)$ is such that $W(x, y) \to +\infty$, as $x, y \to +\infty$, $W(x, y) \to +\infty$ as $x, y \to 0$, and $LW \leq \alpha W$, the proof of (4.8) is achieved by considering that for any t:

$$P(\tau_n \leq t) \leq \exp(\alpha t) \cdot E(W(x_0, y_0)) \cdot (\inf_{\|(x,y)\| > n} W(x, y))^{-1} \tag{4.10}$$

and letting $n \to \infty$ (see the next lemma and theorem, for the definition of the constant α); here $\tau = \inf\{t \geq 0 : \|(x, y)\| \geq n\}$. The equality (4.9) follows from the following:

$$P(\tau_\delta \leq t) \leq \exp(\alpha t) \cdot E(W(x_0, y_0)) \cdot (\inf_{(x,y) \in \Delta} W(x, y))^{-1} \tag{4.11}$$

and letting $\delta \to 0$; here $\Delta = \{(x, y) : 0 < x < \delta; 0 < y < \delta\}$ and $\tau_\delta = \inf\{t \geq 0 : x(t) = \delta \text{ or } y(t) = \delta\}$. (For more details, see [16].)

Actually, our aim is to prove an existence result for Eqs. (4.3) by using Theorem 4.1. First, we observe that for the function V defined in (4.5) we have

$$\lim_{x,y \to +\infty} V(x, y) = +\infty; \quad V(x, y) < (x - x^*) + (y - y^*) \quad \begin{array}{l}\text{for large } x, y \text{ (at the} \\ \text{most, linear growth).}\end{array}$$
$$\tag{4.12}$$

Now, if we split the right member of Eq. (4.6) into different pieces and take into account the definition of $q(x)$ (2.22), and the conditions (C1), (C2), (C3), we easily find that positive constants k, k' and $\varrho > 2r$ exist such that

$$LV(x, y) \leq k \quad \text{for } 0 \leq x, y < \varrho$$
$$LV(x, y) \leq k'[(x - x^*) + (y - y^*)] \quad \text{for } x, y \geq \varrho. \tag{4.13}$$

From this follows that, for $x, y \geq \varrho$ a constant $k'' > 0$ exists such that $LV(x, y) < k'' V(x, y)$.

We observe that the constants k, k', k'' depend on r (which is fixed). Thus, we can conclude:

Lemma 4.2. *With regard to the function defined in (4.5), and to the infinitesimal generator (4.4) associated to Eq. (4.3), positive constants, k, k'' exist such that*

$$LV(x, y) \leq k + k'' V(x, y), \quad \forall (x, y) \in R^+ \times R^+. \tag{4.14}$$

Now, we state the existence theorem:

Theorem 4.3. *We suppose that conditions* $(C1)$, $(C2)$, $C3)$ *hold; then the equations* (4.3) *define a regular diffusion process in the open set* $\Omega = \{(x, y) \in R^2 : x > 0, y > 0\}$ *in connection with any initial condition* (x_0, y_0) *such that* $P\{x_0 > 0, y_0 > 0\} = 1$. *They also define a regular diffusion on both open half axes* $\{x > 0, y = 0\}$ *and* $\{x = 0, y > 0\}$ *for any initial condition such that* $P\{y_0 = 0\} = 1$, $P\{x_0 > 0\} = 1$, *and respectively,* $P\{x_0 = 0\} = 1$, $P\{y_0 > 0\} = 1$. *They also admit the solution* $x = y \equiv 0$.

Proof. We set $\{K_n\}$ a sequence of compact growing sets such that $\bigcup_{n \in N} K_n = \Omega = \{(x, y) \in R^2 : x > 0, y > 0\}$. It is easy to see that the function V defined in (4.5) satisfies (ii) of Theorem 4.1. Although $LV(x, y)$ is not bounded on Ω, thanks to Lemma 4.2, if we say $W(x, y) = k + k''V(x, y)$, we have $LW = k''LV \leqslant k''(k + k''V) = k''W$, that is $LW \leqslant k''W$, $\forall (x, y) \in \Omega$; thus, condition (i) of Theorem 4.1, with $V = W$, holds. So, this proves the first part of the theorem which refers to the diffusion in Ω.

The same arguments apply if we consider the restriction of (4.3) to the half axis $\{x > 0, y = 0\}$ and $\{x = 0, y > 0\}$. For this purpose, it is enough to consider, respectively, the functions:

$$V_1(x) = (x - x^*) - x^* \ln(x/x^*), \qquad V_2(y) = (y - y^*) - y^* \ln(y/y^*).$$

Remark 4.5. The half axis $\{x > x_0, y = 0\}$ is invariant under the evolution with the initial condition $x(0) = x_0 > 0$, $y_0 = 0$, and the process $x(t)$ follows the Gompertz law, in mean. Analogously, the y half axis is invariant under the evolution with initial value $x_0 = 0$, and the predator becomes extinguished (in mean) with exponential rate.

Remark 4.6. Theorem 4.3 implies that probabilities of extinction for each or for both species whose evolutions are given by Eqs. (4.3) are zero (see also the discussion at the beginning of Sect. 4).

Remark 4.7. If we consider Eqs. (2.23), instead of (4.3), Lemma 4.2 also holds for $x, y > \delta$, for any $\delta > 0$ fixed.

Then, by using (4.10), every solution starting from $x(0), y(0) > \delta$ and such that $x(t), y(t) > \delta \ \forall t \geqslant 0$, exists for all time (i.e., there is no explosion) and, for the arbitrariness of δ, any solution starting from positive values remains in the set

$$\Omega^+ = \{x, y \in R^2 : x \geqslant 0, y \geqslant 0\}.$$

The result concerning the impossibility of the solution reaching the axes in a finite time cannot be achieved by using (4.11). Indeed, the first time when the solution reaches one of the bounds $\{x = \delta, y > \delta\}$, $\{x > \delta, y = \delta\}$ cannot be estimated by using (4.11), since the constant k is really a function of δ and, for $\delta \to 0$, $k(\delta)$ grows to infinity. Hence, if we use Eq. (2.23) we obtain the existence result, but we cannot exclude that the solution $(x(t), y(t))$ crosses the axes in a finite time and therefore, in this case, we are not able to conclude that the extinction probabilities are zero. This is the reason why conditions (C1), (C2), (C3) have been supposed to hold.

Remark 4.8. One can consider simpler equations similar to Eqs. (2.23), that is

$$dx_t = (x_t q(x_t) - \gamma x_t y_t)\, dt + b_1(x_t, y_t)\, dW_t^1$$
$$dy_t = y_t(-s + \gamma x_t)\, dt + b_2(x_t, y_t)\, dW_t^2 \qquad (4.15)$$
$$x(0) = x_0, \qquad y(0) = y_0,$$

which describe the randomization of a deterministic predator-prey model in the special case $c = 1$ (eaten prey fully converted into biomass for predators), having as fluctuations (diffusion) terms some functions $b_i(x_t, y_t)$.

In the case when

$$\sup_x [b_i(x)/x_i] < +\infty, \quad i = 1, 2 \qquad (4.16)$$

one can obtain, as well as the existence and uniqueness of the solution, also the existence of a unique ergodic probability measure invariant with respect to (x_t, y_t), by means of another theorem by Khas'minskij (see, e.g., [5], [12]).

Our diffusion terms (4.2) do not satisfy (14.16); indeed, for instance, $(1/x)$ $(x|q(x)| + \gamma xy)^{1/2}$ is not bounded on the curve $y = x^2$. In our case, we are not able to obtain the existence of the above mentioned ergodic probability measure.

5. Numerical simulation

5.1. Numerical treatment of the equations

In this section we deal with the numerical solution of the SDEs (2.23) with initial conditions $x(0) = x_0$, $y(0) = y_0$. Referring to general d-dimensional Itô's SDEs

$$dx_t = a(t, x_t)\, dt + \sigma(t, x_t)\, dW_t, \qquad (5.1)$$

the simplest integration method to find an approximate solution $\bar{x}_{t_i}$ is the stochastic Euler method:

$$\bar{x}_{t_{i+1}} = \bar{x}_{t_i} + a(t_i, \bar{x}_{t_i})h + \sigma(t_i, \bar{x}_{t_i})\, \Delta W_t, \qquad (5.2)$$

where $h = t_{i+1} - t_i$ is the step of integration, $\Delta W_{t_i} = W_{t_{i+1}} - W_{t_i}$ is the corresponding increment of the Wiener process, and $\bar{x}_t$ represents the approximation to the solution x_t. By using the results in [26], one can show that the best integration method for Eq. (2.23) is realized by the Euler scheme with a step error of order h^2, that is $E(\bar{x}_t - x_t)^2 = O(h^2)$.

Therefore, to solve Eq. (2.23) numerically, we used the following scheme:

$$\bar{x}_{i+1} = \bar{x}_i + [\bar{x}_i q(\bar{x}_i) - \bar{y}_i \gamma \bar{x}_i]h + (\bar{x}_i|q(\bar{x}_i)| + \bar{y}_i \bar{y} \bar{x}_i)^{1/2}\, \Delta W_1^1$$
$$\bar{y}_{i+1} = \bar{y}_i + [\bar{y}_i(-s + c\gamma \bar{x}_i)]h + (\bar{y}_i(s + c\gamma \bar{x}_i))^{1/2}\, \Delta W_i^2 \qquad (5.3)$$
$$\bar{x}_0 = x_0, \qquad \bar{y}_0 = y_0.$$

The increments ΔW_i have been calculated by means of the NORMCO routine of the CERN Program Library, which generates Gaussian distributed pseudo-random numbers with given mean and standard deviation.

5.2. Numerical results

Relatively to the choice $q(x) = q_2(x)$ (see (2.21)), we have computed by means of the scheme (5.3) the approximating solution of Eq. (2.23) with given initial data.
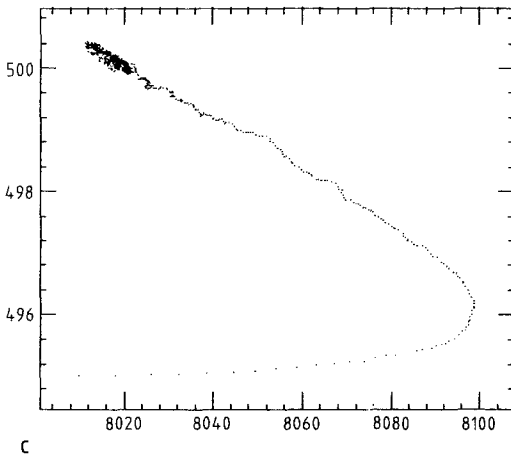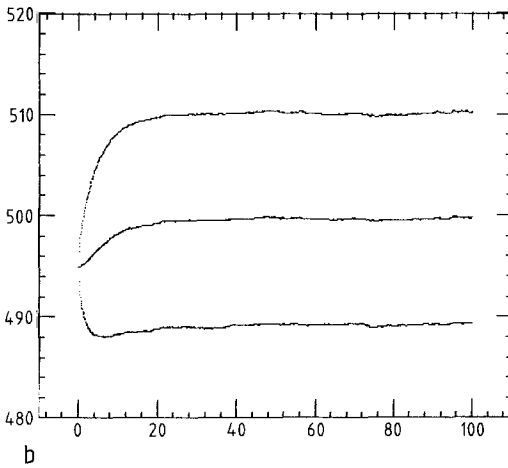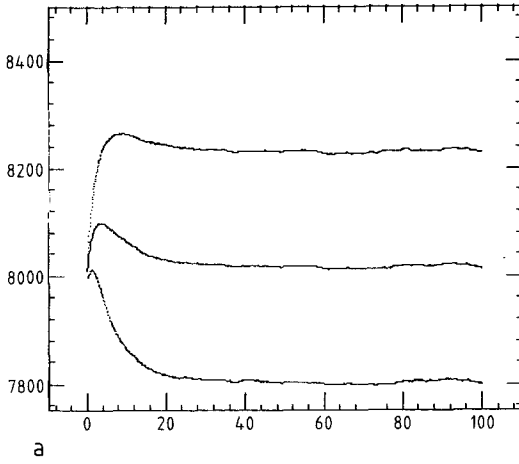
Fig. 1. $q(x) = \lambda b_0 \ln(K/x)$;
$b_0 = [\ln(Kc\gamma/s)]^{-1}$; $\lambda = 1.$; $\gamma = 0.002$;
$s = 0.08$; $c = 0.005$; $K = 30000$;
$x(0) = 8010$; $y(0) = 495$; $M = 40\,000$.
a Plot of $\hat{E}(x(t))$ as function of t
(middle curve); the upper and lower
curve represent, respectively,
$\hat{E}(x(t)) \pm (1/2)(\hat{\text{Var}}\, x(t))^{1/2}$; **b** the
same thing for $y(t)$; **c** plot of the
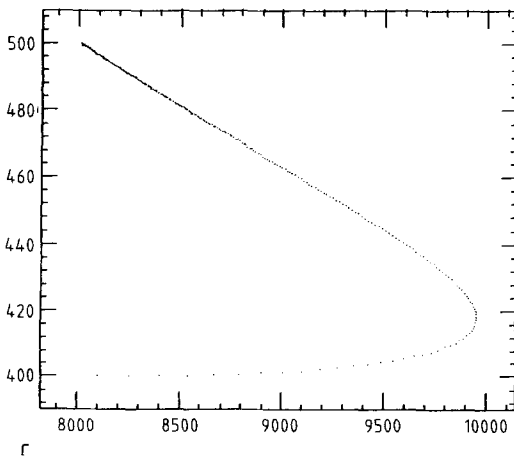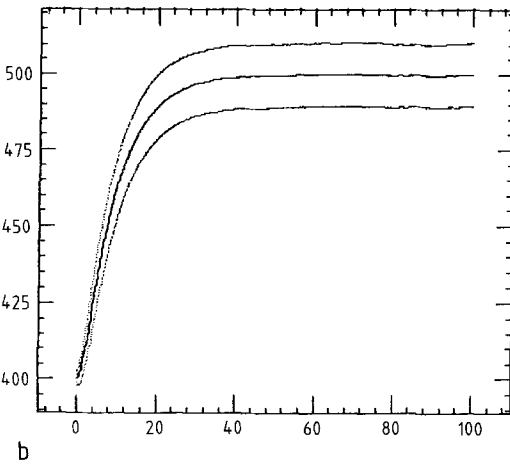trajectory $(\hat{E}(x(t)), \hat{E}(y(t)))$ as
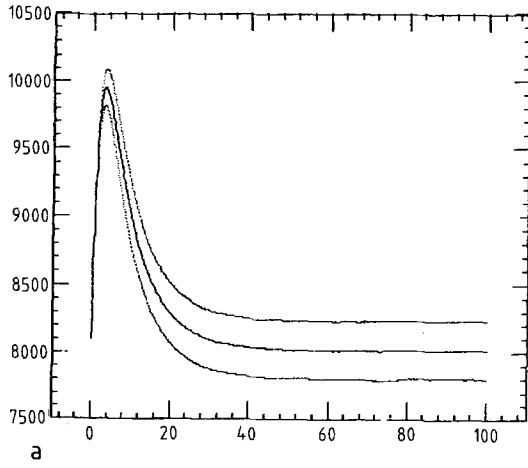function of t, in the phase plane

Fig. 2. $x(0) = 8100$; $y(0) = 400$ (the others parameters as in Fig. 1). **a**–**c** as in Fig. 1a–c
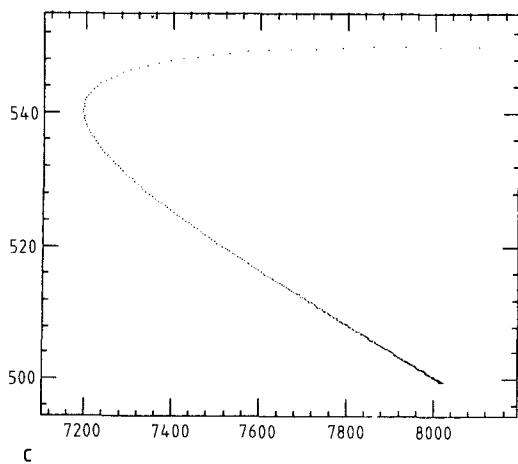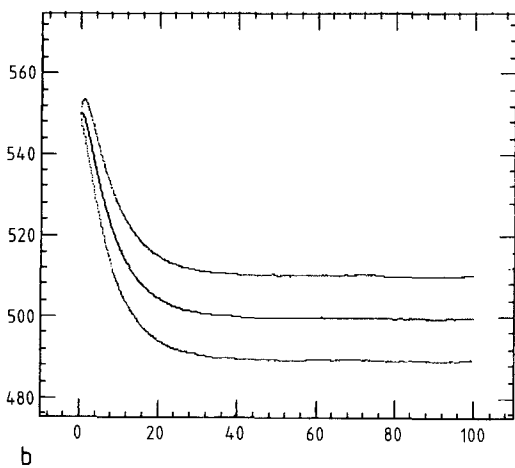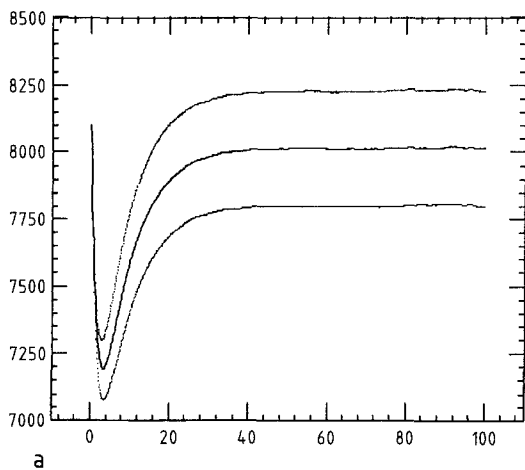
Fig. 3. $x(0) = 8100$; $y(0) = 550$ (the other parameters as in Fig. 1). **a–c** as in Fig. 1a–c

For some initial conditions, a great number of simulation runs has been performed to estimate expectation values $E(x(t))$, $E(y(t))$, and corresponding variances $\text{Var}(x(t))$, $\text{Var}(y(t))$, as functions of t. These estimates have been achieved by means of the estimators:

$$\hat{E}(z(t)) = 1/M \sum_{v=1,\ldots,M} z^v(t)$$

$$\hat{\text{Var}}(z(t)) = 1/M \sum_{v=1,\ldots,M} [z^v(t) - \hat{E}(z(t))]^2, \qquad z = x \text{ or } y$$

where M is the number of simulation runs, and $z^v(t)$ represents, for every t, the approximated value of $z(t)$ obtained by means of vth simulation run.

In some of the enclosed graphs (see Figs. 1, 2, 3) the shapes of $\hat{E}(x(t))$, $\hat{E}(y(t))$ are plotted as functions of t together with error bars for every $0 \leqslant t \leqslant 100$. Indeed, in these graphs, the middle curve represents the estimated expectation value as a function of t; the upper and lower curves represent, respectively.

$$\hat{E}(z)(t)) \pm (1/2)(\hat{\text{Var}}\, z(t))^{1/2}, \quad z = x \text{ or } y.$$

For each of the considered initial conditions, we have performed 40 000 simulation runs spending about 7 h C.P.U. time of a MICRO VAX II computer.

Numerical solutions of Eqs. (2.23) agree with the stochastic stability of the equilibrium point (x^*, y^*) of the deterministic part of those equations, although small perturbations of initial data are reflected by fairly large absolute deviations on solutions (especially prey), fot t small. (Indeed, one can make those deviations small if one takes initial conditions sufficiently close to the equilibrium point.) However we can see that, also for fairly large perturbations of initial data, as t gets large, the solution $(x(t), (y))$ approaches the equilibrium point (x^*, y^*).

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