



# Environmental Brownian noise suppresses explosions in population dynamics

Xuerong Mao, Glenn Marion\*, Eric Renshaw

*Department of Statistics and Modelling Science, University of Strathclyde, Glasgow G1 1XH, UK*

Received 24 September 2000; received in revised form 8 July 2001; accepted 23 July 2001

## Abstract

Population systems are often subject to environmental noise, and our aim is to show that (surprisingly) the presence of even a tiny amount can suppress a potential population explosion. To prove this intrinsically interesting result, we stochastically perturb the multivariate deterministic system  $\dot{x}(t) = f(x(t))$  into the Itô form  $dx(t) = f(x(t))dt + g(x(t))dw(t)$ , and show that although the solution to the original ordinary differential equation may explode to infinity in a finite time, with probability one that of the associated stochastic differential equation does not. © 2001 Published by Elsevier Science B.V.

**Keywords:** Brownian motion; Stochastic differential equation; Explosion; Boundedness; Itô's formula

## 1. Introduction

Single-species deterministic population dynamics can often be described by the ordinary differential equation  $\dot{x} = f(x)$ , and to avoid an explosion (i.e. infinite population size at a finite time)  $f(x)$  has to satisfy certain conditions. Consider, for example, the one-dimensional logistic (i.e. quadratic) equation

$$\dot{x}(t) = x(t)[b + ax(t)] \quad (1)$$

on  $t \geq 0$  with initial value  $x(0) = x_0 > 0$ . Since here the variable  $x(t)$  denotes population size, only positive solutions are of interest. For parameters  $a < 0$  and  $b > 0$ , Eq. (1) has the global solution

$$x(t) = \frac{b}{-a + e^{-bt}(b + ax_0)/x_0} \quad (t \geq 0),$$

which is not only positive and bounded but also has the asymptotic property that  $\lim_{t \rightarrow \infty} x(t) = b/|a|$ . In contrast, if we now let  $a > 0$ , whilst retaining  $b > 0$ , then Eq. (1) has only the local solution

$$x(t) = \frac{b}{-a + e^{-bt}(b + ax_0)/x_0} \quad (0 \leq t < T),$$

\* Corresponding author. Current address: Biomathematics & Statistics Scotland, University of Edinburgh, James Clerk Maxwell Building, The King's Buildings, Edinburgh EH9 3DH, UK.

E-mail address: glenn@bioss.ac.uk (G. Marion).

1 which explodes to infinity at the finite time

$$T = -\frac{1}{b} \log \left( \frac{ax_0}{b + ax_0} \right).$$

However, given that population systems are often subject to environmental noise, it  
 3 is important to discover whether the presence of such noise affects this result. Suppose  
 that the parameter  $a$  is stochastically perturbed, with

$$a \rightarrow a + \varepsilon \dot{w}(t),$$

5 where  $\dot{w}(t)$  is white noise and  $\varepsilon > 0$  represents the intensity of the noise. Then this  
 environmentally perturbed system may be described by the Itô equation

$$dx(t) = x(t)[(b + ax(t))dt + \varepsilon x(t)dw(t)]. \quad (2)$$

7 In this paper, we shall show that with probability one the solution of Eq. (2) can no  
 longer explode in a finite time if  $a > 0$ . In summary, when  $a > 0$  and  $\varepsilon = 0$  the solution  
 9 explodes at the finite time  $t = T$ ; whilst conversely, no matter how small  $\varepsilon > 0$ , the  
 solution will not explode in a finite time. In other words, stochastic environmental  
 11 noise suppresses deterministic explosion.

Given the nature of this potentially counter-intuitive result, it is worthwhile presenting  
 13 a simple illustration before we proceed to the general proof. For  $0 < h \ll 1$  consider  
 the discrete-time system

$$x(t+h) = x(t) + hx(t)(1+x(t)) + \sqrt{h}x^2(t)z(t), \quad (3)$$

15 where, for some constant  $d > 0$ ,  $\{z(t)\}$  denotes the Bernoulli noise process

$$\Pr(z(t) = d) = \Pr(z(t) = -d) = 0.5.$$

This system is an appropriate simplification as, in the limit  $h \rightarrow 0$ , it tends towards an  
 17 Itô equation of the form (2). Note that the noise intensity is represented by  $d$ , in other  
 words  $\sqrt{h}z(t) \rightarrow \varepsilon d\omega(t)$ . On denoting the ‘reaction’ component  $\theta(t) \equiv hx(t)(1+x(t))$   
 19 and ‘noise’ component  $\phi(t) \equiv \sqrt{h}x^2(t)z(t)$ , we see that for  $x(t) > \hat{x} \equiv \sqrt{h}/(d - \sqrt{h}) \simeq$   
 $\sqrt{h}/d$  we have  $\phi(t) > \theta(t)$ , whence negative  $z(t)$  result in downwards increments. This  
 21 suggests that for  $x(t)$  near  $\hat{x}$  the process might exhibit local stability. Moreover, for

$$x(t) > \hat{x} = \frac{1+h}{\sqrt{hd}-h} \simeq \frac{1}{\sqrt{hd}}$$

a negative  $z(t)$ -value results in  $x(t+h) < 0$ . So the existence of our environmental  
 23 noise  $\{z(t)\}$  places an effective upper bound on  $\{x(t)\}$ , since for  $x(t) > \hat{x}$  the process  
 becomes negative after a further geometric (0.5) distributed number of steps. This is  
 25 highly suggestive of our main result since, once the population grows sufficiently large,  
 the noise will eventually cause a catastrophic population crash.

For  $h = 10^{-4}$  we found that for one simulation  $d$  had to be as high as 5 to ensure that  
 27  $x(t)$  remained positive over  $0 \leq t \leq 100$  (Fig. 1a), which suggests that nonnegativity is  
 29 associated with early domination of the deterministic logistic term by the environmental  
 noise. This ties in with known results in population dynamics, for which persistence  
 31 is associated with the avoidance of ‘boom-and-bust’ dynamics. Note that  $x(t)$  exhibits  
 ‘epidemic’-like behaviour, spending most of the time hovering around a relatively low

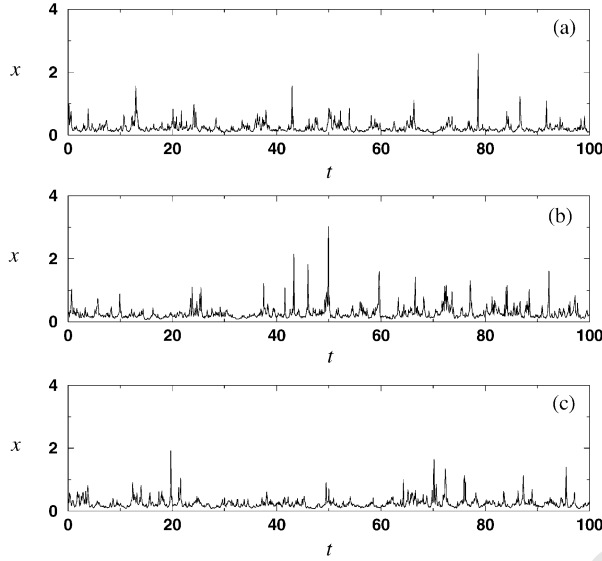


Fig. 1. Graph (a) shows a realization of the discrete-time system (3) for  $d = 5$  and  $h = 10^{-4}$ . Graphs (b) and (c) show the same system for  $h = 10^{-6}$  and  $10^{-8}$ , respectively.

‘endemic’ level with occasional upward surges. Moreover, over the time range shown,  $x(t)$  substantially exceeds  $\hat{x} = 0.002$ , so  $\hat{x}$  does *not* relate to local equilibrium levels; whilst  $x(t) < 3.0$  remains considerably less than the critical value  $\tilde{x} = 20$ . The role of  $h$  can be seen by running the simulation over  $0 \leq t \leq 1000$ , since (for this given run)  $x(t)$  became negative even when  $d = 100$ , though persistence was achieved by decreasing  $h$  to  $10^{-6}$ . Figs. 1b and c show  $x(t)$  for  $h = 10^{-6}$  and  $10^{-8}$ , respectively, sampled at  $t = 0, 0.01, \dots, 100$ , and visual comparison between all three shows little evidence that the structure of sampled  $x(t)$ -values depends on  $h$ . A question of considerable interest is whether one can determine the limiting distribution of  $\{x(t) | x(t) > 0\}$  as  $h \rightarrow 0$ .

This behavioural stability can be shown (informally) by considering a small fixed time interval  $(s, s + \tau)$  over which  $x(t) \simeq x(s)$  (i.e. changes little). Then as the variance of each step increment is  $\simeq (\sqrt{h}x^2(s)d)^2/2$ , and there are  $\tau/h$  independent steps, the displacement variance for time length  $\tau$  is  $(hx^4(s)d^2/2) \times (\tau/h) = x^4(s)d^2\tau/2$  which is clearly independent of  $h$ . It is interesting to note that this stability occurs only because the environmental noise takes order  $O(\sqrt{h})$ ; for any other order either the reaction or the environmental components will become totally dominant as  $h \rightarrow 0$ .

More practically, let us now consider bivariate systems. When there are no interspecific interactions, a bounded system can be described by the purely logistic scheme

$$\begin{aligned}\dot{x}_1(t) &= x_1(t)[b_1 - a_{11}x_1(t)], \\ \dot{x}_2(t) &= x_2(t)[b_2 - a_{22}x_2(t)]\end{aligned}\tag{4}$$

for positive parameters  $b_1$ ,  $b_2$ ,  $a_{11}$  and  $a_{22}$ . However, if each species enhances the growth of the other, then the interactive dynamics are governed by the coupled ordinary

1 differential equations

$$\begin{aligned}\dot{x}_1(t) &= x_1(t)[b_1 - a_{11}x_1(t) + a_{12}x_2(t)], \\ \dot{x}_2(t) &= x_2(t)[b_2 - a_{22}x_2(t) + a_{21}x_1(t)],\end{aligned}\tag{5}$$

where  $a_{12}, a_{21} > 0$ . This type of ecological interaction is known as facultative mutualism; that is, each species enhances the growth of the other although each species can persist in the absence of the other. There exists an extensive literature concerned with the dynamics of mutualism (cf. Boucher, 1985; He and Gopalsamy, 1997; Wolin and Lawlor, 1984). In general,  $a_{12}, a_{21}$  are assumed to be smaller than  $a_{11}, a_{22}$ , e.g.  $a_{12}a_{21} < a_{11}a_{22}$ , otherwise the solution of Eq. (5) may explode at a finite time. For example, consider the symmetric system

$$\begin{aligned}\dot{x}_1(t) &= x_1(t)[1 - x_1(t) + 2x_2(t)], \\ \dot{x}_2(t) &= x_2(t)[1 - x_2(t) + 2x_1(t)].\end{aligned}\tag{6}$$

9 If we let the initial values be the same, e.g.  $x_1(0) = x_2(0) = 1$ , then by symmetry  $x_1(t) = x_2(t)$ . Thus

$$\dot{x}_1(t) = x_1(t)[1 + x_1(t)],$$

11 which has the solution

$$x_1(t) = \frac{1}{-1 + 2e^{-t}} \quad (0 \leq t < \log(2))$$

with explosion at  $t = \log(2)$ . However, this situation will change significantly if there is environmental noise. To be precise, let such a system be governed by the Itô equation

$$\begin{aligned}dx_1(t) &= x_1(t)[(b_1 - a_{11}x_1(t) + a_{12}x_2(t))dt + (\varepsilon_{11}x_1(t) + \varepsilon_{12}x_2(t))dw(t)], \\ dx_2(t) &= x_2(t)[(b_2 - a_{22}x_2(t) + a_{21}x_1(t))dt + (\varepsilon_{21}x_1(t) + \varepsilon_{22}x_2(t))dw(t)].\end{aligned}\tag{7}$$

We shall see that for arbitrary parameters  $b_i, a_{ij}$ , system (7) will not explode in a finite time with probability 1 provided the noise intensities  $\varepsilon_{11}, \varepsilon_{22} > 0$  and  $\varepsilon_{12}, \varepsilon_{21} \geq 0$ .

## 2. Noise suppresses explosion

Throughout this paper, unless otherwise specified, we let  $(\Omega, \mathcal{F}, \{\mathcal{F}_t\}_{t \geq 0}, P)$  be a complete probability space with a filtration  $\{\mathcal{F}_t\}_{t \geq 0}$  satisfying the usual conditions (i.e. it is right continuous and  $\mathcal{F}_0$  contains all  $P$ -null sets). Let  $w(t)$  denote one-dimensional Brownian motion defined on this probability space. If  $A$  is a vector or matrix, its transpose is denoted by  $A^T$ . If  $A$  is a matrix, its trace norm is denoted by  $|A| = \sqrt{\text{trace}(A^T A)}$  whilst its operator norm is denoted by  $\|A\| = \sup\{|Ax| : |x| = 1\}$ . We also introduce the notation  $\mathbb{R}_+^n = \{x \in \mathbb{R}^n : x_i > 0 \text{ for all } 1 \leq i \leq n\}$ .

Consider the Lotka–Volterra model for a system with  $n$  interacting components, namely

$$\dot{x}_i(t) = x_i(t) \left( b_i + \sum_{j=1}^n a_{ij} x_j \right) \quad (1 \leq i \leq n).$$

Define  $\text{diag}(x_1(t), \dots, x_n(t))$  as the  $n \times n$  matrix with all elements zero except those on the diagonal which are  $x_1(t), \dots, x_n(t)$ . Then the Lotka–Volterra model takes the matrix form

$$\dot{x}(t) = \text{diag}(x_1(t), \dots, x_n(t)) [b + Ax(t)], \quad (8)$$

where

$$x = (x_1, \dots, x_n)^T, \quad b = (b_1, \dots, b_n)^T, \quad A = (a_{ij})_{n \times n}$$

and  $a_{ij}$  denotes the element in the  $i$ th row and  $j$ th column of an  $n \times n$  matrix. Suppose that every parameter  $a_{ij}$  is stochastically perturbed, with

$$a_{ij} \rightarrow a_{ij} + \sigma_{ij} \dot{w}(t).$$

Then Eq. (8) takes the stochastic form

$$dx(t) = \text{diag}(x_1(t), \dots, x_n(t)) [(b + Ax(t)) dt + \sigma x(t) dw(t)], \quad (9)$$

where  $\sigma = (\sigma_{ij})_{n \times n}$ . Since the purpose of this paper is to discover the effect of environmental noise, we naturally impose the following simple hypothesis on the noise intensities,

(H1)  $\sigma_{ii} > 0$  if  $1 \leq i \leq n$  whilst  $\sigma_{ij} \geq 0$  if  $i \neq j$ .

As the  $i$ th state  $x_i(t)$  of Eq. (9) is the size of the  $i$ th component in the system, it should be nonnegative. Moreover, in order for a stochastic differential equation to have a unique global (i.e. no explosion in a finite time) solution for any given initial value, the coefficients of the equation are generally required to satisfy the linear growth condition and local Lipschitz condition (cf. Mao, 1997). However, the coefficients of Eq. (9) do not satisfy the linear growth condition, though they are locally Lipschitz continuous, so the solution of Eq. (9) may explode at a finite time. In this section, we shall show that under the simple hypothesis (H1) the solution of Eq. (9) is positive and global. This result reveals the important property that the environmental noise suppresses the explosion, as suggested by the stochastic simulation shown in Section 1.

**Theorem 2.1.** *Under hypothesis (H1), for any system parameters  $b \in \mathbb{R}^n$ ,  $A \in \mathbb{R}^{n \times n}$ , and any given initial value  $x_0 \in \mathbb{R}_+^n$ , there is a unique solution  $x(t)$  to Eq. (9) on  $t \geq 0$  and the solution will remain in  $\mathbb{R}_+^n$  with probability 1, namely  $x(t) \in \mathbb{R}_+^n$  for all  $t \geq 0$  almost surely.*

**Proof.** Since the coefficients of the equation are locally Lipschitz continuous, for any given initial value  $x_0 \in \mathbb{R}_+^n$  there is a unique local solution  $x(t)$  on  $t \in [0, \tau_e)$ , where  $\tau_e$  is the explosion time (cf. Arnold, 1972 or Friedman, 1976). To show this solution is global, we need to show that  $\tau_e = \infty$  a.s. Let  $k_0 > 0$  be sufficiently large for every

- 1 component of  $x_0$  lying within the interval  $[1/k_0, k_0]$ . For each integer  $k \geq k_0$ , define the stopping time

$$\tau_k = \inf\{t \in [0, \tau_e) : x_i(t) \notin (1/k, k) \text{ for some } i = 1, \dots, n\},$$

- 3 where throughout this paper we set  $\inf \emptyset = \infty$  (as usual  $\emptyset$  denotes the empty set). Clearly,  $\tau_k$  is increasing as  $k \rightarrow \infty$ . Set  $\tau_\infty = \lim_{k \rightarrow \infty} \tau_k$ , whence  $\tau_\infty \leq \tau_e$  a.s. If we  
 5 can show that  $\tau_\infty = \infty$  a.s., then  $\tau_e = \infty$  a.s. and  $x(t) \in \mathbb{R}_+^n$  a.s. for all  $t \geq 0$ . In other words, to complete the proof all we need to show is that  $\tau_\infty = \infty$  a.s. For if this  
 7 statement is false, then there is a pair of constants  $T > 0$  and  $\varepsilon \in (0, 1)$  such that

$$P\{\tau_\infty \leq T\} > \varepsilon.$$

Hence there is an integer  $k_1 \geq k_0$  such that

$$P\{\tau_k \leq T\} \geq \varepsilon \quad \text{for all } k \geq k_1. \quad (10)$$

- 9 Define a  $C^2$ -function  $V : \mathbb{R}_+^n \rightarrow \mathbb{R}_+$  by

$$V(x) = \sum_{i=1}^n [\sqrt{x_i} - 1 - 0.5 \log(x_i)].$$

The nonnegativity of this function can be seen from

$$\sqrt{u} - 1 - 0.5 \log(u) \geq 0 \quad \text{on } u > 0.$$

- 11 If  $x(t) \in \mathbb{R}_+^n$ , the Itô formula shows that

$$\begin{aligned} dV(x(t)) &= \sum_{i=1}^n \left\{ 0.5(x_i^{-0.5} - x_i^{-1})x_i \left[ \left( b_i + \sum_{j=1}^n a_{ij}x_j \right) dt + \sum_{j=1}^n \sigma_{ij}x_j dw(t) \right] \right. \\ &\quad \left. + 0.5(-0.25x_i^{-1.5} + 0.5x_i^{-2})x_i^2 \left[ \sum_{j=1}^n \sigma_{ij}x_j \right]^2 dt \right\} \\ &= \sum_{i=1}^n \left\{ 0.5(x_i^{0.5} - 1) \left( b_i + \sum_{j=1}^n a_{ij}x_j \right) + (0.25 - 0.125x_i^{0.5}) \left[ \sum_{j=1}^n \sigma_{ij}x_j \right]^2 \right\} dt \\ &\quad + \sum_{i=1}^n \sum_{j=1}^n 0.5(x_i^{0.5} - 1)\sigma_{ij}x_j dw(t), \end{aligned}$$

where we write  $x(t) = x$ . Compute

$$\begin{aligned} &\sum_{i=1}^n (x_i^{0.5} - 1) \left( b_i + \sum_{j=1}^n a_{ij}x_j \right) \\ &\leq \sum_{i=1}^n |b_i|(x_i^{0.5} + 1) + \sum_{i=1}^n \sum_{j=1}^n |a_{ij}|x_j + \sum_{i=1}^n \sum_{j=1}^n |a_{ij}|x_i^{0.5}x_j \end{aligned}$$

$$\begin{aligned}
&\leq \sum_{i=1}^n |b_i|(x_i^{0.5} + 1) + \sum_{j=1}^n \sum_{i=1}^n |a_{ij}|x_j + \sum_{i=1}^n \sum_{j=1}^n 0.5|a_{ij}|(x_i + x_j^2) \\
&= \sum_{i=1}^n \left( |b_i|(1 + x_i^{0.5}) + \sum_{j=1}^n (|a_{ji}| + 0.5|a_{ij}|)x_i + 0.5 \sum_{j=1}^n |a_{ji}|x_i^2 \right)
\end{aligned}$$

1 and

$$\sum_{i=1}^n \left[ \sum_{j=1}^n \sigma_{ij}x_j \right]^2 \leq \sum_{i=1}^n \left[ \sum_{j=1}^n \sigma_{ij}^2 \sum_{j=1}^n x_j^2 \right] = |\sigma|^2 \sum_{i=1}^n x_i^2.$$

Moreover, by hypothesis (H1),

$$\sum_{i=1}^n x_i^{0.5} \left[ \sum_{j=1}^n \sigma_{ij}x_j \right]^2 \geq \sum_{i=1}^n \sigma_{ii}^2 x_i^{2.5}.$$

3 So

$$\begin{aligned}
&\sum_{i=1}^n \left\{ 0.5(x_i^{0.5} - 1) \left( b_i + \sum_{j=1}^n a_{ij}x_j \right) + (0.25 - 0.125x_i^{0.5}) \left[ \sum_{j=1}^n \sigma_{ij}x_j \right]^2 \right\} \\
&\leq \sum_{i=1}^n \left\{ 0.5|b_i|(1 + x_i^{0.5}) + \sum_{j=1}^n (0.5|a_{ji}| + 0.25|a_{ij}|)x_i \right. \\
&\quad \left. + 0.25 \left( \sum_{j=1}^n |a_{ji}| + |\sigma|^2 \right) x_i^2 - 0.125\sigma_{ii}^2 x_i^{2.5} \right\},
\end{aligned}$$

which is bounded, say by  $K$ , in  $\mathbb{R}_+^n$ . We therefore obtain

$$\int_0^{\tau_k \wedge T} dV(x(t)) \leq \int_0^{\tau_k \wedge T} K dt + \int_0^{\tau_k \wedge T} \sum_{i=1}^n \sum_{j=1}^n 0.5(x_i^{0.5} - 1)\sigma_{ij}x_j dw(t)$$

5 since  $x(t \wedge \tau_k) \in \mathbb{R}_+^n$ . Whence taking expectations, yields

$$EV(x(\tau_k \wedge T)) \leq V(x_0) + KE(\tau_k \wedge T) \leq V(x_0) + KT. \quad (11)$$

Set  $\Omega_k = \{\tau_k \leq T\}$  for  $k \geq k_1$  and, by (10),  $P(\Omega_k) \geq \varepsilon$ . Note that for every  $\omega \in \Omega_k$ ,

7 there is some  $i$  such that  $x_i(\tau_k, \omega)$  equals either  $k$  or  $1/k$ , and hence  $V(x(\tau_k, \omega))$  is no less than either

$$\sqrt{k} - 1 - 0.5 \log(k)$$

9 or

$$\sqrt{1/k} - 1 - 0.5 \log(1/k) = \sqrt{1/k} - 1 + 0.5 \log(k).$$

Consequently,

$$V(x(\tau_k, \omega)) \geq [\sqrt{k} - 1 - 0.5 \log(k)] \wedge [0.5 \log(k) - 1].$$

1 It then follows from (11) that

$$\begin{aligned} V(x_0) + KT &\geq E[1_{\Omega_k}(\omega)V(x(\tau_k, \omega))] \\ &\geq \varepsilon([\sqrt{k} - 1 - 0.5 \log(k)] \wedge [0.5 \log(k) - 1]), \end{aligned}$$

where  $1_{\Omega_k}$  is the indicator function of  $\Omega_k$ . Letting  $k \rightarrow \infty$  leads to the contradiction

$$\infty > V(x_0) + KT = \infty$$

3 so we must therefore have  $\tau_\infty = \infty$  a.s.  $\square$

It is easy to see from this theorem that, with probability 1, neither Eq. (2) nor (7) will explode in a finite time, as stated earlier in Section 1.

### 3. Boundedness

7 Theorem 2.1 shows that under the simple hypothesis (H1) the positive cone  $\mathbb{R}_+^n$  is the invariant set of the solutions of Eq. (9). In the sequel we therefore only need to consider how the solutions vary in  $\mathbb{R}_+^n$ . Let us denote by  $x(t; x_0)$  the unique global solution of Eq. (9) given initial value  $x(0) = x_0$ . For convenience, let us define the diffusion operator  $L$  acting on  $C^2$ -functions  $V \in C^2(\mathbb{R}_+^n; R)$  by

$$\begin{aligned} LV(x) &= V_x(x) \text{diag}(x_1, \dots, x_n)(b + Ax) \\ &\quad + \frac{1}{2} x^T \sigma^T \text{diag}(x_1, \dots, x_n) V_{xx}(x) \text{diag}(x_1, \dots, x_n) \sigma x, \end{aligned}$$

where

$$V_x = (V_{x_1}, \dots, V_{x_n}) \quad \text{and} \quad V_{xx} = (V_{x_i x_j})_{n \times n}.$$

13 **Theorem 3.1.** *Let hypothesis (H1) hold. Let  $\theta_1, \dots, \theta_n$  be positive numbers such that*

$$\theta_1 + \dots + \theta_n < \frac{1}{2}. \quad (12)$$

Then, for any initial value  $x_0 = (x_{01}, \dots, x_{0n})^T \in \mathbb{R}_+^n$ , the solution  $x(t; x_0) = x(t)$  of Eq. (9) has the property that

$$\log \left( E \left[ \prod_{i=1}^n x_i^{\theta_i}(t) \right] \right) \leq e^{-c_1 t} \sum_{i=1}^n \theta_i \log x_{0i} + \frac{c_2}{c_1} (1 - e^{-c_1 t}) \quad \text{for all } t \geq 0, \quad (13)$$

where

$$c_1 = \frac{1}{4} \left( 1 - \sum_{i=1}^n \theta_i \right) \min_{1 \leq i \leq n} \theta_i \sigma_{ii}^2 \quad \text{and} \quad c_2 = |\theta| \|b\| + \frac{|\theta|^2 \|A\|^2}{4c_1}.$$

17 In particular, letting  $t \rightarrow \infty$  in (13) yields the asymptotic estimate

$$\limsup_{t \rightarrow \infty} E \left( \prod_{i=1}^n x_i^{\theta_i}(t) \right) \leq e^{c_2/c_1}. \quad (14)$$

To prove this theorem consider the following lemma.



- 1 **Lemma 3.2.** *Let hypothesis (H1) hold, and  $\theta^T = (\theta_1, \dots, \theta_n)$  be positive numbers such that*

$$\theta_1 + \dots + \theta_n < 1. \quad (15)$$

- 3 *Then, for any initial value  $x_0 \in \mathbb{R}_+^n$ , the solution  $x(t; x_0) = x(t)$  of Eq. (9) has the property that*

$$E \left( \prod_{i=1}^n x_i^{\theta_i}(t) \right) < \infty \quad \text{for all } t \geq 0. \quad (16)$$

- 5 **Proof.** Define a  $C^2$ -function  $V: \mathbb{R}_+^n \rightarrow \mathbb{R}_+$  by

$$V(x) = \prod_{i=1}^n x_i^{\theta_i}.$$

It is not difficult to show that

$$LV(x) = V(x)\theta^T(b + Ax) - \frac{1}{2}V(x)x^T\sigma^T[\text{diag}(\theta_1, \dots, \theta_n) - \theta\theta^T]\sigma x. \quad (17)$$

- 7 Note that for any  $y = (y_1, \dots, y_n)^T \in \mathbb{R}^n$ ,

$$\begin{aligned} y^T[\text{diag}(\theta_1, \dots, \theta_n) - \theta\theta^T]y &= \sum_{i=1}^n \theta_i y_i^2 - \left( \sum_{i=1}^n \theta_i y_i \right)^2 \\ &\geq \sum_{i=1}^n \theta_i y_i^2 - \sum_{i=1}^n \theta_i \sum_{i=1}^n \theta_i y_i^2 = \left( 1 - \sum_{i=1}^n \theta_i \right) \sum_{i=1}^n \theta_i y_i^2. \end{aligned}$$

Thus, for  $x \in \mathbb{R}_+^n$ ,

$$\begin{aligned} x^T\sigma^T[\text{diag}(\theta_1, \dots, \theta_n) - \theta\theta^T]\sigma x &\geq \left( 1 - \sum_{i=1}^n \theta_i \right) \sum_{i=1}^n \theta_i \left( \sum_{j=1}^n \sigma_{ij} x_j \right)^2 \\ &\geq \left( 1 - \sum_{i=1}^n \theta_i \right) \sum_{i=1}^n \theta_i \sigma_{ii}^2 x_i^2 \\ &\geq \left( 1 - \sum_{i=1}^n \theta_i \right) \left( \min_{1 \leq i \leq n} \theta_i \sigma_{ii}^2 \right) |x|^2 = 4c_1 |x|^2, \end{aligned}$$

- 9 where  $c_1$  is defined in the statement of Theorem 3.1. It then follows from (17) that

$$LV(x) \leq V(x)[|\theta|(|b| + \|A\||x|) - 2c_1|x|^2].$$

Since

$$|\theta|\|A\||x| \leq \frac{|\theta|^2\|A\|^2}{4c_1} + c_1|x|^2.$$

- 11 We therefore obtain

$$LV(x) \leq V(x)[c_2 - c_1|x|^2], \quad (18)$$

- 1 where  $c_2$  is defined in the statement of Theorem 3.1. For every integer  $k \geq 1$ , define the stopping time

$$\tau_k = \inf\{t \geq 0: |x(t)| \geq k\},$$

- 3 which by Theorem 2.1 has the properties that,  $\tau_k < \infty$  and  $\tau_k \rightarrow \infty$  almost surely as  $k \rightarrow \infty$ . Now for any  $t \geq 0$ , the Itô formula shows that

$$V(x(t \wedge \tau_k)) = V(x_0) + \int_0^{t \wedge \tau_k} LV(x(s)) ds + \int_0^{t \wedge \tau_k} V(x(s)) \theta^T \sigma x(s) dw(s).$$

- 5 Taking expectations of both sides and making use of (18) yields

$$EV(x(t \wedge \tau_k)) \leq V(x_0) + c_2 E \int_0^{t \wedge \tau_k} V(x(s)) ds \leq V(x_0) + c_2 \int_0^t EV(x(s \wedge \tau_k)) ds,$$

whence applying the well-known Gronwall inequality gives

$$EV(x(t \wedge \tau_k)) \leq V(x_0) e^{c_2 t}.$$

- 7 Letting  $k \rightarrow \infty$  shows that

$$EV(x(t)) \leq V(x_0) e^{c_2 t} \quad (t \geq 0)$$

and the required assertion follows.  $\square$

- 9 **Proof of Theorem 3.1.** We use the same notation as in the proof of Lemma 3.2, which shows that  $EV(x(t))$  is finite for all  $t \geq 0$ . Moreover, by Theorem 2.1,  $V(x(t)) > 0$  with probability 1, so we must have  $EV(x(t)) > 0$  for all  $t \geq 0$ . In addition, the continuity of  $EV(x(t))$  in  $t$  can be seen by the continuity of the solution  $x(t)$  and the dominated convergence theorem. For convenience, let us set

$$v(t) = EV(x(t)) \quad \text{for } t \geq 0.$$

- 15 Then  $v(t)$  is a continuous positive function of  $t \geq 0$ . Define the right upper derivative of  $v(t)$  by

$$D_+ v(t) = \limsup_{\delta \downarrow 0} \frac{v(t + \delta) - v(t)}{\delta} \quad (t \geq 0).$$

We claim that

$$D_+ v(t) \leq v(t)(c_1 + c_2 - c_1 v(t)) \quad (t \geq 0). \quad (19)$$

- 17 To show this, note that

$$V(x) \leq \prod_{i=1}^n |x|^{\theta_i} = |x|^{\theta_1 + \dots + \theta_n} \leq 1 + |x|^2.$$

Then it follows from (18) that

$$LV(x) \leq V(x)[c_1 + c_2 - c_1(1 + |x|^2)] \leq V(x)[c_1 + c_2 - c_1 V(x)]. \quad (20)$$

- 19 On recalling condition (12), namely that  $\theta_1 + \dots + \theta_n < 1$ , we observe from Lemma 3.2 that

$$EV^2(x(t)) < \infty \quad \text{for all } t \geq 0.$$

- 1 Whence it follows from the Itô formula and (20) that for any  $t \geq 0$  and  $\delta > 0$ ,

$$EV(x(t + \delta)) - EV(x(t)) \leq \int_t^{t+\delta} [(c_1 + c_2)EV(x(s)) - c_1 EV^2(x(s))] ds.$$

- 3 Using the Hölder inequality which implies that  $EV(x(s)) \leq [EV^2(x(s))]^{1/2}$ , we then have

$$EV(x(t + \delta)) - EV(x(t)) \leq \int_t^{t+\delta} [(c_1 + c_2)EV(x(s)) - c_1 [EV(x(s))]^2] ds$$

that is

$$v(t + \delta) - v(t) \leq \int_t^{t+\delta} [(c_1 + c_2)v(s) - c_1 [v(s)]^2] ds.$$

- 5 Dividing both sides by  $\delta$  and letting  $\delta \downarrow 0$  yields the claimed inequality (19). We now compute the derivative

$$\begin{aligned} D_+[e^{c_1 t} \log v(t)] &= c_1 e^{c_1 t} \log v(t) + e^{c_1 t} \frac{D_+ v(t)}{v(t)} \\ &\leq c_1 e^{c_1 t} \log v(t) + e^{c_1 t} [c_1 + c_2 - c_1 v(t)]. \end{aligned}$$

- 7 Noting that  $\log v(t) \leq v(t) - 1$  we obtain

$$D_+[e^{c_1 t} \log v(t)] \leq c_2 e^{c_1 t},$$

whence integration yields

$$e^{c_1 t} \log v(t) \leq \log v(0) + \frac{c_2}{c_1} [e^{c_1 t} - 1].$$

- 9 Consequently,

$$\log v(t) \leq e^{-c_1 t} \log v(0) + \frac{c_2}{c_1} [1 - e^{-c_1 t}],$$

which is the required assertion (13), while the other assertion (14) follows by letting

11  $t \rightarrow \infty$ .  $\square$

#### 4. Generalizations

- 13 Eq. (9) arises from Eq. (8) by assuming that the system matrix  $A$  is stochastically perturbed, with  $A \rightarrow A + \sigma \dot{w}(t)$ . We may assume that both the system vector  $b$  and  
15 the matrix  $A$  are stochastically perturbed, with

$$b \rightarrow b + \beta \dot{w}_1(t) \quad \text{and} \quad A \rightarrow A + \sigma \dot{w}_2(t),$$

where  $w_1(t)$  and  $w_2(t)$  are two independent Brownian motions and  $\beta = (\beta_1, \dots, \beta_n)^T$ ,

- 17 whilst  $\sigma$  is the same as before. Then Eq. (8) takes the stochastic form

$$\dot{x}(t) = \text{diag}(x_1(t), \dots, x_n(t))[(b + Ax(t))dt + \beta dw_1(t) + \sigma x(t) dw_2(t)]. \quad (21)$$

More generally, consider a system taking the form

$$19 \quad \dot{x}(t) = \text{diag}(x_1(t), \dots, x_n(t))[f(x)dt + g(x)dw(t)], \quad (22)$$

where  $w(t) = (w_1(t), \dots, w_2(t))^T$  is now an  $m$ -dimensional Brownian motion while  $f: \mathbb{R}_+^n \rightarrow \mathbb{R}^n$  and  $g: \mathbb{R}_+^n \rightarrow \mathbb{R}^{n \times m}$ . Clearly, Eq. (21) is a special case of Eq. (22), with  $f(x) = b + Ax$ ,  $g(x) = (\beta, \sigma x)$  and  $w(t) = (w_1(t), w_2(t))^T$ . Let  $f_i$  be the  $i$ th component of  $f$  and  $g_i$  the  $i$ th row of  $g$ . Then we impose the following hypothesis on the coefficients:

(H2) Both  $f$  and  $g$  are locally Lipschitz continuous. Moreover, there are constants  $h_1, h_2, \alpha_1 > 0$  and  $\alpha_2 \geq 0$  such that

$$|f(x)| \leq h_1(1 + |x|) \quad \text{and} \quad \alpha_1 x_i^2 - \alpha_2 \leq |g_i(x)|^2 \leq h_2(1 + |x|^2)$$

for all  $x \in \mathbb{R}_+^n$  and  $1 \leq i \leq n$ .

**Theorem 4.1.** Under hypothesis (H2), for any given initial value  $x_0 \in \mathbb{R}_+^n$ , there is a unique solution  $x(t)$  to Eq. (22) on  $t \geq 0$  and the solution will remain in  $\mathbb{R}_+^n$  with probability 1, namely  $x(t) \in \mathbb{R}_+^n$  for all  $t \geq 0$  almost surely.

**Proof.** The theorem can be proved in the same way as for the proof of Theorem 2.1.

Retaining the same notations, we can show by the Itô formula that

$$\begin{aligned} dV(x(t)) &= \sum_{i=1}^n [0.5(x_i^{0.5} - 1)f_i(x) + (0.25 - 0.125x_i^{0.5})|g_i(x)|^2] dt \\ &\quad + \sum_{i=1}^n 0.5(x_i^{0.5} - 1)g_i(x) dw(t) \end{aligned}$$

whenever  $x(t) = x \in \mathbb{R}_+^n$ . Applying hypothesis (H2) then yields

$$dV(x(t)) \leq K dt + \sum_{i=1}^n 0.5(x_i^{0.5} - 1)g_i(x) dw(t)$$

for some  $K > 0$ . The remainder of the proof is the same as before.  $\square$

We can also extend Theorem 3.1 to Eq. (22) as described below.

**Theorem 4.2.** Let hypothesis (H2) hold. Let  $\theta_1, \dots, \theta_n$  be positive numbers such that

$$\theta_1 + \dots + \theta_n < \frac{1}{2}. \quad (23)$$

Then, for any initial value  $x_0 = (x_{01}, \dots, x_{0n})^T \in \mathbb{R}_+^n$ , the solution  $x(t; x_0) = x(t)$  of Eq. (22) has the property that

$$\begin{aligned} \log \left( E \left[ \prod_{i=1}^n x_i^{\theta_i}(t) \right] \right) &\leq e^{-\hat{\theta} x_1 t / 4} \sum_{i=1}^n \theta_i \log x_{0i} \\ &\quad + \frac{4K}{\hat{\theta} \alpha_1} \left( 1 - e^{-\hat{\theta} x_1 t / 4} \right) \quad \text{for all } t \geq 0, \end{aligned} \quad (24)$$

where

$$\hat{\theta} = \left( 1 - \sum_{i=1}^n \theta_i \right) \min_{1 \leq i \leq n} \theta_i \quad \text{and} \quad K = \hat{\theta} \left( h_1 + \frac{h_1}{2\alpha_1} + \frac{n\alpha_2}{2} \right).$$

1 In particular, letting  $t \rightarrow \infty$  in (24) yields the asymptotic result

$$\limsup_{t \rightarrow \infty} E \left( \prod_{i=1}^n x_i^{\theta_i}(t) \right) \leq e^{4K/\hat{\theta}\alpha_1}. \quad (25)$$

**Proof.** The diffusion operator  $L$  associated with Eq. (22) has the form

$$LV(x) = V_x(x) \text{diag}(x_1, \dots, x_n) f(x) + \frac{1}{2} \text{trace}[g^T(x) \text{diag}(x_1, \dots, x_n) V_{xx}(x) \text{diag}(x_1, \dots, x_n) g(x)].$$

3 Applying this to the  $C^2$ -function  $V: \mathbb{R}_+^n \rightarrow \mathbb{R}_+$  defined by

$$V(x) = \prod_{i=1}^n x_i^{\theta_i}$$

gives

$$LV(x) = V(x) \theta^T f(x) - \frac{1}{2} V(x) \text{trace}(g^T(x) [\text{diag}(\theta_1, \dots, \theta_n) - \theta \theta^T] g(x)),$$

5 where  $\theta = (\theta_1, \dots, \theta_n)^T$  as before. It is not difficult to see from the proof of Lemma 3.2 that

$$\text{trace}(g^T(x) [\text{diag}(\theta_1, \dots, \theta_n) - \theta \theta^T] g(x)) \geq \hat{\theta} |g(x)|^2 = \hat{\theta} \sum_{i=1}^n |g_i(x)|^2.$$

7 This, together with hypothesis (H2), yields

$$\text{trace}(g^T(x) [\text{diag}(\theta_1, \dots, \theta_n) - \theta \theta^T] g(x)) \geq \hat{\theta} \alpha_1 |x|^2 - n \hat{\theta} \alpha_2.$$

So on using (H2) once again,

$$LV(x) \leq V(x) \left[ h_1 \hat{\theta} (1 + |x|) - \frac{1}{2} (\hat{\theta} \alpha_1 |x|^2 - n \hat{\theta} \alpha_2) \right] \leq V(x) \left[ K - \frac{\hat{\theta} \alpha_1}{4} |x|^2 \right].$$

9 This takes the same form as Eq. (18), and the remainder of the proof parallels that of Theorem 3.1.  $\square$

## 11 5. Examples and computer simulations

13 In this section, we explore system behaviour using numerical solutions of the stochastic differential system (22). In particular, for  $t = \Delta t, 2\Delta t, \dots$ , we employ the Euler scheme

$$x_{\Delta t}(t + \Delta t) = \text{diag}((x_{\Delta t})_1(t), \dots, (x_{\Delta t})_n(t)) [f(x_{\Delta t}(t)) \Delta t + g(x_{\Delta t}(t)) \Delta w(t)] \quad (26)$$

15 with initial condition  $x(0) \in \mathbb{R}_+^n$  and time increment  $\Delta t$ . For each time step the vector  $\Delta w(t) = (\Delta w(t)_1, \dots, \Delta w(t)_m)^T$  represents  $m$  independent draws from a normal distribution with zero mean and variance  $\Delta t$ . Recent results by Marion et al. (2001) show that, for any finite time and a sufficiently small time step, this numerical scheme will  
17 converge to the true solution of (22) provided that a  $C^2$  function  $V: \mathbb{R}_+^n \rightarrow \mathbb{R}_+$  exists and satisfies the following conditions:  
19

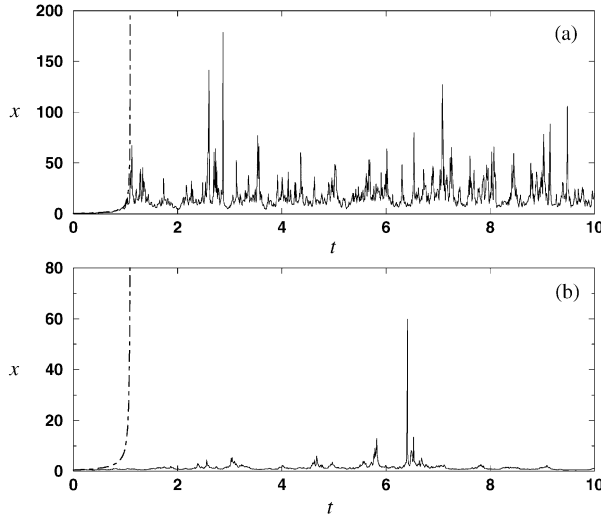


Fig. 2. In graph (a) the solid curve shows a stochastic trajectory generated by the Euler scheme for time step  $\Delta t = 10^{-7}$  and  $\sigma = 0.25$  for a one-dimensional system (9) with  $A = b = 1$ . The corresponding deterministic trajectory is shown by the dot-dashed curve. In Graph (b)  $\sigma = 1.0$ .

- 1 (i) the set  $\mathcal{D}(r) = \{x \in \mathbb{R}_+^n : V(x) \leq r\}$  is compact for any  $r > 0$ ;
- 2 (ii)  $LV(x) \leq K(1 + V(x))$ ;
- 3 (iii) there exists a positive constant  $K_2(\mathcal{D}(r))$  such that for all  $x, y \in \mathcal{D}(r)$

$$|V(x) - V(y)| \vee |V_x(x) - V_x(y)| \vee |V_{xx}(x) - V_{xx}(y)| \leq K_3(\mathcal{D}(r))|x - y|.$$

The function  $V(x)$  defined in the proof of Theorem 2.1 satisfies each of these conditions, and so the Euler scheme may be applied with confidence to the generalized system (22), and hence also to (9).

Fig. 2 shows the results from simulation runs based on the Euler scheme for a one-dimensional example of system (9) with  $A = b = 1$ , the initial condition  $x_0 = 0.5$  and  $\Delta t = 10^{-7}$ . Fig. 2a shows a realization of the dynamics of this system for  $\sigma = 0.25$ , whilst Fig. 2b corresponds to  $\sigma = 1.0$ . In each case the corresponding prediction of the deterministic model, which explodes at  $t \approx 1.0986$ , is also shown. These simulations illustrate the main result of this paper, namely that environmental noise suppresses population explosion in such systems. Moreover, comparison of Figs. 2a and b suggests that fluctuations reduce as the noise level increases.

Finally, consider the bivariate system

$$\begin{aligned} dx_1(t) &= x_1(1 - x_1 + 2x_2)dt + \varepsilon x_1^2 d\omega_1(t), \\ dx_2(t) &= x_2(1 - 2x_2 + 2x_1)dt + 2\varepsilon x_2^2 d\omega_2(t), \end{aligned} \quad (27)$$

which is of the generalized form (22). Fig. 3 shows a realization of the numerical solution of this system based on the Euler scheme, with time step  $\Delta t = 10^{-4}$  and noise level  $\varepsilon = 1.0$ . Comparison with the deterministic solution (also shown) supports the conclusion of Theorem 4.1, namely that noise suppresses the population explosion.

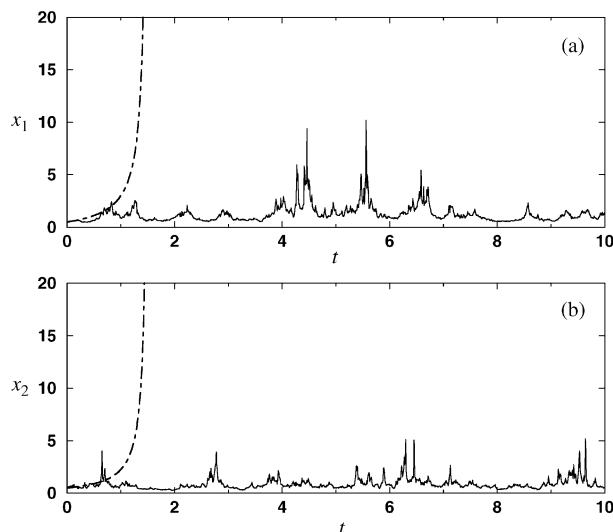


Fig. 3. In both graphs the solid curve represents a stochastic trajectory for system (27) generated by the Euler scheme with time step  $\Delta t = 10^{-4}$  and  $\varepsilon = 1.0$ , whilst the corresponding deterministic solution is shown by the dot-dashed curve. Graph (a) shows the first component  $x_1$  and graph (b) the second,  $x_2$ .

## 6. Uncited References

Butler et al., 1986; Hutson and Schmitt, 1992; Jansen, 1987; Khasminskii, 1981; Kifer, 1990; Kirlinger, 1988; Ladde and Lakshmikantham, 1980; Liptser and Shiryaev, 1989; Mao, 1991; Mao, 1994; Ramanan and Zeitouni, 1999.

## Acknowledgements

The authors would like to thank the BBSRC and EPSRC for their financial support under Grant 78/MMI09712, and in addition, the editor and an anonymous referee for their helpful comments on the manuscript.

## References

- Arnold, L., 1972. Stochastic Differential Equations: Theory and Applications. Wiley, New York.
- Boucher, D.H. (Ed.), 1985. The Biology of Mutualism. Groom Helm, London.
- Butler, G., Freedman, H.I., Waltman, P., 1986. Uniformly persistence systems. Proc. Amer. Math. Soc. 96, 425–430.
- Friedman, A., 1976. Stochastic Differential Equations and their Applications. Academic Press, New York.
- He, X., Gopalsamy, K., 1997. Persistence, attractivity, and delay in facultative mutualism. J. Math. Anal. Appl. 215, 154–173.
- Hutson, V., Schmitt, K., 1992. Permanence and the dynamics of biological systems. Math. Biosci. 111, 1–71.
- Jansen, W., 1987. A permanence theorem for replicator and Lotka–Volterra system. J. Math. Biol. 25, 411–422.
- Khasminskii, R.Z., 1981. Stochastic Stability of Differential Equations. Sijthoff and Noordhoff, Alphen a/d Rijn.

- 1 Kifer, Y., 1990. Principal eigenvalues, topological pressure, and stochastic stability of equilibrium states.  
Isreal J. Math. 70, 1–47.
- 3 Kirlinger, G., 1988. Permanence of some ecological systems with several predator and one prey species.  
J. Math. Biol. 26, 217–232.
- 5 Ladde, G.S., Lakshmikantham, V., 1980. Random Differential Inequalities. Academic Press, New York.
- 7 Liptser, R.Sh., Shirayev, A.N., 1989. Theory of Martingales. Kluwer Academic Publishers, Dordrecht  
(Translation of the Russian edition, Nauka, Moscow, 1986).
- 9 Mao, X., 1991. Stability of Stochastic Differential Equations with Respect to Semimartingales. Longman  
Scientific and Technical, New York.
- 11 Mao, X., 1994. Exponential Stability of Stochastic Differential Equations. Marcel Dekker, New York.
- 13 Mao, X., 1997. Stochastic Differential Equations and Applications. Horwood, New York.
- 15 Marion, G., Mao, X., Renshaw, E., 2001. Convergence of the Euler scheme for a class of stochastic  
differential equation. Internat. Math. J., in press.
- 17 Ramanan, K., Zeitouni, O., 1999. The quasi-stationary distribution for small random perturbations of certain  
one-dimensional maps. Stochastic Process. Appl. 86, 25–51.
- Wolin, C.L., Lawlor, L.R., 1984. Models of facultative mutualism: density effects. Amer. Natrual. 124,  
843–862.