## Coloured-noise-induced transitions in nonlinear structures<sup>\*</sup>

Romi Mankin, Tõnu Laas, Erkki Soika, Ako Sauga, Astrid Rekker, Ain Ainsaar, Ülo Ugaste

**Abstract.** In a stochastic framework, macroscopic approaches are sought to describe microscopic interaction between different species. Coloured-noise-induced transitions in stochastic *N*-species Lotka-Volterra systems are considered analytically as an appropriate model extendable to many natural and nano-technological processes. All the results discussed are computed by means of a dynamical mean-field approximation. It is demonstrated that interplay of coloured noise and interaction intensities of species can generate a variety of cooperation effects, such as discontinuous transitions of the mean population density, noise-induced Hopf bifurcations and relaxation oscillation. The necessary conditions for the cooperation effects are also discussed. Particularly, it is established that, in the case of the Beddington functional response, in certain parameter regions of the model an increase in noise correlation time can cause multiple transitions (more than two) between relaxation oscillatory regimes and equilibrium states.

**Key words:** non-equilibrium fluctuations • coloured-noise-induced transitions • mean-field approximation • Hopf bifurcation • stochastic Lotka-Volterra system

R. Mankin, T. Laas<sup>∞</sup>, E. Soika, A. Sauga, A. Rekker,
A. Ainsaar, Ü. Ugaste
Tallinn University,
25 Narva Road, 10120 Tallinn, Estonia,
Tel.: +372 6409 410, Fax: +372 6409 418,
E-mail: tony@tlu.ee

Received: 14 January 2008 Accepted: 3 July 2008

### Introduction

Fundamental research of stochastic process in materials under the influence of high heat plasma and hard radiation pulses is important for a number of fields of technology – nuclear fission and fusion, air-space technology, accelerator engineering, etc. In the framework of denoted topics, the elaboration of a phenomenological model of interaction between dense plasma beams and construction materials is of special interest [12, 23]. Investigation of stochastic processes in the nonlinear systems, in particular diffusion, non-equilibrium phase transitions, noise-induced patterns formation, etc. is closely concerned with this problem [2, 3, 5, 7].

In recent years, an increasing interest has been shown in noise-induced non-equilibrium phenomena in spatially extended systems [10], of which stochastic resonance [9], noise-induced phase transitions [10], stochastic transport in ratchets [24], noise-induced spatial patterns, and travelling structures [10] are a few examples. Active analytical and numerical investigations of various models in this field have been stimulated by their possible applications in population biology [27], molecular biology, chemical physics, nanotechnology, and for separation techniques of nanoobjects [13, 24].

<sup>\*</sup> Presented on 3rd Research Coordination Meeting on Dense Magnetized Plasmas, 9–13 April 2007, Beijing, China.

Over the last years various noise processes with arbitrary correlation time have been in use in a wide variety of problems in physical, chemical and biological sciences. Among other forms, dichotomous noise [11] is a typical theoretician's paradigm for environmental fluctuations in this context. Environmental fluctuations modelled as dichotomous noise are also the topic of the present paper.

We consider non-equilibrium transitions in N-species stochastic Lotka-Volterra systems of interacting populations, i.e. in systems, which are described by non-negative integers counting the members of different species acting within the problem scope. Molecules, atoms, photons, particles of plasma, predators and preys, infected individuals, etc., all can be regarded as populations under a diversity of situations [10, 11]. The different nature of the systems will become apparent by the characteristic interactions of each particular problem under consideration. The model presented in this paper can be rather considered as a toy-model for the elaboration of the above-mentioned phenomenological model of interaction between plasma beams and construction materials. However, we prefer here the biological interpretation of the model, because our results are immediately applicable in the ecosystem context.

The purpose of the present paper is twofold: first, to provide a compact review of a series of our recently published papers [14, 17-21, 25], in which the colourednoise-induced transitions in nonlinear structures were considered. And second, to discuss - on the basis of the proposed model-system - some novel phenomena in stochastic systems where the role of the noise correlation time as a control parameter is crucial. We are reporting here the following results for the stochastic predator-prey models with the Beddington functional response: (i) we establish coloured-noise-induced transitions from a globally stable equilibrium to the stable limit cycle (with some oscillations of population abundances), as well as in the opposite direction; (ii) the transition is found to be re-entrant, i.e. if the noise amplitude is greater than a certain threshold value, then the limit cycle appears above a critical value of the noise correlation time, but disappears again through re-entrant transition to the equilibrium state at a higher value of the noise correlation time; (iii) for certain parameters of the Beddington functional response there appear two re-entrant transitions (between oscillatory regimes and equilibrium states) vs. noise correlation time. It seems that the behaviour mentioned last is a new noise-induced phenomenon for stochastic preypredator systems.

In particular, we show that the proposed simple toymodel exhibits a variety of unexpected non-equilibrium cooperation effects, including noise-induced single and doubly unidirectional abrupt transitions, as well as noise-induced Hopf bifurcations.

#### A model with dichotomous noise

The present model is based on a generalization of the Lotka-Volterra model to the case of one predator population and *N* prey populations:

(1) 
$$\frac{dX_i}{dt} = X_i \left[ f_i \left( X_i \right) - \frac{y}{\overline{x}} g\left( \overline{x}, y \right) \right],$$
$$\frac{dy}{dt} = y \left[ \frac{\beta}{\alpha} g\left( \overline{x}, y \right) - d \right]$$

where  $X_i(t)$  (i = 1,...,N) is the density of the *i*-th prey population at the time t, y(t) is the density of the predator population, and  $\bar{x}(t) = (1/N) \cdot \Sigma_i X_i(t)$  is the average of the prey population densities. The non-negative constants  $\beta$ , *d* and  $\alpha$  stand for the predator growth rate, the predator death rate, and the prey capturing rate, respectively.

The function  $f(X_i)$  describes the development of the *i*-th species without any interaction with other species. A typical mechanism for the self-regulation within ecosystems includes, for example, territorial breeding requirements and the crowding effect caused by competition for resources. This is taken into account by applying the generalized Verhulst model

(2) 
$$f_i(X_i) = \delta \left[ 1 - \left( \frac{X_i}{K_i} \right)^c \right]$$

where c > 0 and  $\delta > 0$  are constants, and  $K_i$  is the carrying capacity of the *i*-th species. It is remarkable that Gompertz self-regulation  $\tilde{f}(X)$  is a special limit of generalized Verhulst self-regulation Eq. (2), namely

(3) 
$$\lim_{c \to 0, \delta \to \infty} \tilde{f}_i(X) = -\tilde{\delta} \ln\left(\frac{X}{K_i}\right), \ \tilde{\delta} = \delta c = \text{const}$$

Without any loss of generality we may confine ourselves to time units with  $\delta = 1$  or ( $\tilde{\delta} = 1$ ). Random interaction with the environment is taken into account by introducing a coloured noise in  $f_i(X_i)$ . From now on we shall use fluctuations of the carrying capacity

(4) 
$$K_i = K \left[ 1 - \varepsilon \overline{x} \right] \left[ 1 + a_0 Z_i(t) \right]$$

where the factor  $[1 - \varepsilon x]$ ,  $\varepsilon \ge 0$ , mimics a decrease of the carrying capacity caused by adaptive competition of populations for common resources, while coloured noise  $Z_i(t)$  is assumed to be a dichotomous Markovian stochastic process [11]. A dichotomous process is a random stationary Markovian process consisting of jumps between two values z = -1, 1. The jumps follow in time according to a Poisson process, while the values occur with the stationary probability  $\frac{1}{2}$ . The mean value of  $Z_i(t)$  and the correlation function are

(5) 
$$\langle Z_i(t) \rangle = 0, \ \langle Z_i(t) Z_j(t') \rangle = \delta_{ij} \exp(-v|t-t'|)$$

where  $\delta_{ij}$  is the Kronecker symbol and the switching rate v is the reciprocal of the noise correlation time  $v = 1/\tau_c$ . Obviously, model (1) with Eqs. (2) and (4) is biologically meaningful only if  $a_0 < 1$ .

The function g(x,y) is given by

(6)

$$g(x, y) = \frac{x(\alpha - Jx^2)}{x + by + e}$$

where  $\alpha \ge 0, J \ge 0, b \ge 0$ , and  $e \ge 0$  are constants. The functional response g(x,y) is quite general:

- (i) if J = 0, then g(x,y) is the Beddington functional response [4], which describes the effect of predator interference on the trophic function. The parameters  $\alpha$ , *b* and *e* stand for the prey capturing rate, predator interference intensity, and a saturation constant, respectively.
- (ii) Most popular functional responses, such as the Holling type II prey-dependent functional response (J = 0, b = 0 in Eq. (6)) [6] and Michaelis-Menten-Holling type ratio-dependent functional response (J = 0, e = 0 in Eq. (6)) [1], are particular cases of Eq. (6).
- (iii) In the case  $\beta = d = \alpha = b = e = 0, y = 1$ , model (1) describes an *N*-species symbiotic ecosystem [8, 14, 19, 25]; the coupling constant J > 0 characterizes the intensity of symbiotic interaction.

To proceed with the analytical examination of model (1) we follow the mean field approximation scheme. We assume that  $N \rightarrow \infty$ . This means that we are interested in the case of a very great number of populations (or subpopulations in a metapopulation). The mean field approximation can be attained by replacing the size average  $\bar{x}$  by the statistical average  $\langle X(t) \rangle$  in Eqs. set (1). For the stationary state (or for the quasi-stationary state), we can solve the master equation corresponding to Eqs. (1), assuming that the predator growth rate is very small,  $\beta \ll 1$ , i.e., y varies very slowly. Since the dynamics of  $X_i$  is much faster than that of y, a quasistationary probability distribution is formed before y is distinctly changed. In other words, the variable y in Eqs. set (1) is just a parameter for the dynamics of  $X_i$ . In this case, we can investigate the mean field dynamics of the Eqs. set (1) using the effective calculation scheme presented in [14, 19–21, 25].

In the mean field approximation,  $\bar{x} = \langle X(t) \rangle$ , each stochastic differential equation for  $X_i(t)$  in Eqs. (1) can be reduced to a stochastic differential equation of the form

(7) 
$$\frac{dX(t)}{dt} = X(t) \left\{ \rho(t) - \gamma X^{c}(t) [1 - aZ(t)] \right\}$$

where

$$\rho(t) = 1 - \frac{y(t)}{\langle X(t) \rangle} g\left(\langle X(t) \rangle, y(t)\right),$$
  

$$\gamma(t) = \frac{1}{2K^{c} \left[1 - \varepsilon \langle X(t) \rangle\right]^{c} (1 - a_{0}^{2})^{c}} \left[(1 + a_{0})^{c} + (1 - a_{0})^{c}\right],$$
  

$$a = \frac{(1 + a_{0})^{c} - (1 - a_{0})^{c}}{(1 + a_{0})^{c} + (1 - a_{0})^{c}}.$$

The corresponding composite master equation is

(8) 
$$\frac{\partial}{\partial t}P_n(x,t) = -\frac{\partial}{\partial x} \left\{ x \left[ \rho - \gamma x^c \left( 1 - a_n \right) \right] P_n(x,t) \right\} - \frac{v}{2} \sum_{m=1}^{2} \left( 2\delta_{nm} - 1 \right) P_m(x,t)$$

with  $P_n(x,t)$  denoting the probability density for the combined process  $(x, a_n, t)$ ; n, m = 1,2; and  $a_1 = -a_2 = a$ .

If the predator population density *y* is a very slow variable (or constant) and  $\rho > 0$ , then significant inequalities follow from Eq. (7) to characterize the quasi-stationary (or stationary) state of the system. For a stationary case,  $x_1 = \rho^{1/c}/[\gamma (1 - a)]^{1/c}$  and  $x_2 = \rho^{1/c}/[\gamma (1 + a)]^{1/c}$  are stable fixed points of the deterministic Eq. (7) with Z(t) = 1 and Z(t) = -1, respectively, and all trajectories X(t) satisfy the following inequalities:

(9) 
$$\left[\frac{\rho}{\gamma(1-a)}\right]^{1/c} > X(t) > \left[\frac{\rho}{\gamma(1+a)}\right]^{1/c}$$

For a stationary state we can solve Eq. (8), taking as the boundary condition that there is no probability current at the boundary (9). With the help of the stationary probability distribution, one can easily calculate the moments of prey population densities

(10) 
$$\left\langle X^{k} \right\rangle = \left(\frac{\rho}{\gamma}\right)^{k/c} {}_{2}F_{1}\left(\frac{k}{2c}, \frac{k}{2c} + \frac{1}{2}; \frac{\nu}{2c\rho} + \frac{1}{2}; a^{2}\right)$$

where  $_2F_1$  is the hypergeometric function and k = 1, 2, ...Thus in the case of k = 1 Eq. (10) with the equation

(11) 
$$\frac{dy}{dt} = y \left[ \frac{\beta}{\alpha} g\left( \langle X \rangle, y \right) - d \right]$$

determine, by small predator growth rates, the selfconsistency equations for the mean field of model (1).

An alternative method to find the statistical average  $\langle X(t) \rangle$ , appropriate to all values of the predator growth rate  $\beta$ , is presented in our work [17], but this method (also briefly described in section: "Noise-controlled Hopf bifurcation") assumes that the noise variance is small.

# Noise-induced discontinuous transitions in systems with symbiotic interaction

The case of generalized Verhulst self-regulation

The presence of coloured fluctuations of the carrying capacities of populations in *N*-species symbiotic systems with generalized Verhulst self-regulation ( $\varepsilon = \beta = d = \alpha = b = e = 0, y = 1$  in Eqs. set (1)) with an exponent c > 1, is analysed and discussed in [19]. We have found that:

- (i) coloured fluctuations of the environment can cause bistability and abrupt transitions of mean population densities;
- (ii) the hysteresis for the mean field and related discontinuous transitions can be found as a function of noise parameters as well as of the coupling constant;
- (iii) for c > 1 abrupt changes of mean population densities appear only if the noise amplitude is greater than the threshold value  $a_{0c}$  and the critical noise amplitude depends on the exponent c, only:  $a_{0c}$ increases relatively rapidly if c increases;
- (iv) in the case of fixed values of *c* there is a lower limit for the coupling parameter  $J^*(c) > 0$ , below which,  $J < J^*(c)$  the system is monostable at all values of the noise parameters.



**Fig. 1.** The mean value of the population density  $\langle X \rangle$  vs. the coupling strength *J* at different correlation times  $\tau_c$ . System parameters: c = 2,  $a_0 = 0.99$ , K = 1, y = 1 and  $\varepsilon = \alpha = b = e = \beta = d = 0$ . In the case of  $\tau_c = 0.5$  the system shows hysteresis. Solid and dashed lines are stable and unstable solutions of the self-consistency equation, respectively.

Figure 1 shows different solutions of the self-consistency equation for the mean value of the population density  $\langle X \rangle$  as a function of the coupling constant J and the noise correlation time  $\tau_c$  at the noise amplitude  $a_0 = 0.99$ . The solid and dashed lines are stable and unstable solutions of the self-consistency equation, respectively. The existence of alternative stable states (Fig. 1, the curve  $\tau_c = 0.5$ ) indicates that there is a coexistence region,  $J_1 < J < J_2$ , where two stable phases are possible. Notably, coexistence does not mean that the two phases are present simultaneously; however, either is possible depending on the initial distribution. If the value of the mean field  $\langle X \rangle$  lies on the lower branch of the curve  $\tau_c = 0.5$  close to the point F, a slight growth of the coupling parameter J induces a catastrophic transition of the system to another stable state with the value of the mean field  $\langle X \rangle$  corresponding to the point G. The opposite shift occurs when the coupling parameter decreases below the value  $J_1$ . The situation described represents a typical case of first-order phase transitions. As the coupling-induced two-phase coexistence region does not exist in the system without noise, it is a coloured-noise-induced effect.

From Fig. 1, one can see that the coexistence region of the two phases exists only for moderate values of the correlation time  $\tau_c$ . Hence, there is an upper limit  $\tau_c^*$  for the correlation time  $\tau_c$ , at greater values of which the system is monostable. In the case of fixed values of cthe critical parameter  $\tau_{c}^{*}$  increases monotonically from zero to infinity, if the noise amplitude  $a_0$  increases from  $a_{0c}$  to one. Noise induced bistability, i.e. hysteresis, can also occur no matter which noise parameter,  $\tau_c$  or  $a_0$ , is chosen as the control parameter. For example, if the noise correlation time  $\tau_c$  is considered as the control parameter, it can be found that a jump from a state with a bigger number of individuals to that with a lesser one occurs at smaller correlation times than the opposite jumps. Perhaps the most important new result, in an ecological context, is the existence of the critical noise amplitude  $a_{0c}(c)$ . We emphasize that for c > 1 abrupt changes of mean population densities appear only if the noise amplitude exceeds the threshold value  $a_{0c}(c)$ . Therefore, as the critical noise amplitude increases relatively rapidly if c increases, it seems reasonable to

assume that in symbiotic ecosystems with generalized Verhulst self-regulation abrupt transitions appear with a greater probability if the exponent c is lower.

The phenomenon of coloured-noise-induced abrupt transitions is robust enough to survive a modification of the noise as well as the self-regulation mechanism. Our calculations (see [14]) analogous to those given in [19] show that in the case of trichotomous noise most of the results of [19] are qualitatively valid. The trichotomous noise [15] consists of jumps between three values:  $z_1 = a$ ,  $z_2 = 0, z_3 = -a$ , while a > 0. The jumps follow, in time, the pattern of a Poisson process, the values occurring with the stationary probabilities  $p_s(a) = p_s(-a) = q$  and  $p_s(0) = 1 - 2q$ , where  $0 < q < \frac{1}{2}$ . In a stationary state the trichotomous process Z(t) satisfies  $\langle Z(t) \rangle = 0$  and  $\langle Z(t + \tau)/Z(t) \rangle = 2qa^2 \exp(-v\tau)$ , where the switching rate v is the reciprocal of the noise correlation time  $\tau_c = 1/\nu$ , i.e., Z(t) is a symmetric zero-mean exponentially correlated Markovian noise. It is remarkable that for a trichotomous noise Z, the kurtosis  $\varphi = (\langle Z^4 \rangle / \langle Z^2 \rangle^2)$ - 3, contrary to the case of symmetric dichotomous noise ( $\varphi = -2$ ), can be anything from -2 to  $\infty$ . Notably, variations of the kurtosis of trichotomous noise can also induce discontinuous transitions.

#### The case of Gompertz self-regulation

We have also modified the self-regulation mechanism. The influence of environmental fluctuations on an N-species symbiotic system with Gompertz self-regulation (Eq. (3)) is discussed in [25]. Though the general picture of the coloured-noise-induced hysteresis is the same as that encountered in [19], some new phenomena appear. We have established two types of noise-induced discontinuous transitions - doubly unidirectional transitions (DUT) and single unidirectional transitions (SUT). Moreover, we have given the necessary and sufficient conditions for the appearance of such effects. SUT means that an increase in noise amplitude can cause a catastrophic fall in the size of populations, while by decreasing the noise amplitude no opposite transitions can occur. To our knowledge, the appearance of a noise-induced SUT in models of ecosystems without extinction is a novel noise-induced effect.

When investigating the dependence of  $\langle X \rangle$  on the correlation time  $\tau_c$ , five qualitatively different types of the graph  $\langle X \rangle$  vs. the switching rate v emerge (Fig. 2). These can be interpreted as different "phases" in the phase space  $(\varepsilon, J)$ , where  $\varepsilon$  is an adaptation parameter (the phases (a)–(e) in Fig. 3): (a) the system is monostable for all values of  $\tau_c$ ; (b) the phenomenon of DUT appears; (c) the system exhibits SUT from a lesser number of individuals to a bigger number; (d) the system exhibits SUT from a bigger number of individuals to a lesser one; (e) in this case, the system is bistable for all values of  $\tau_c$ , no transitions between stable states occur. Note that the coordinates of points B, C, and E in Fig. 3 depend on the noise amplitude  $a_0$ . As  $a_0$  increases from zero to one, the points C and E move away from the origin O and this will increase the region of the phase space  $(\varepsilon, J)$ , where discontinuous transitions are possible. Moreover, the point B moves from A to D, which causes an increase of the domain (d), where



**Fig. 2.** Typical shapes of the function  $\langle X \rangle$  vs. the noise switching rate  $v = 1/\tau_c$  for the different domains in (a), (b), (c), (d), and (e) in Fig. 3. The solid and dashed lines are stable and unstable solutions of the self-consistency equation, respectively. More details are in the text.



**Fig. 3.** ( $\varepsilon$ , *J*) phase diagram for the dependence of the mean value of the population density  $\langle X \rangle$  on  $\tau_c$  in the case of Gompertz self-regulation (Eq. (3)). System parameters:  $a_0 = 0.95$ , K = 1, y = 1,  $\alpha = b = e = \beta = d = 0$ . Discontinuous transitions occur in the regions (a), (b) and (c). More details are in the text.

a SUT from the state of a bigger number of individuals to a lesser one takes place. This novel feature of symbiotic ecosystems can provide a possible scenario for some catastrophic shifts of population sizes observed in nature [26].

The mean-field results considered correspond to an infinite number of globally coupled species. Bearing in mind the results of computer simulations (see [19]), one can assume that this scenario is not much different from more realistic systems, where the number of species is finite, at least in the case when the number of species is large enough.

#### **Noise-controlled Hopf bifurcation**

Recently, we have considered a broad class of (N + 1)-species ratio-dependent predator-prey models. Those consist of one predator population and N prey populations with fluctuating carrying capacities [17]. A special case of this model corresponds to model (1) with  $\varepsilon = J = e = 0$ . Notably, in the framework of the mean field theory it is shown that the dynamical system for the mean prey abundance and predator abundance exhibits Hopf bifurcation with respect to the noise correlation time. The corresponding transitions are found to be re-entrant, e.g., the periodic orbit appears above a critical value of the noise correlation time, but disappears again at a higher value of the noise correlation time. Assuming that the noise variance is small, the nonmonotonous dependence of the critical capturing rate  $\alpha_{cr}(\tau_c)$  on the noise variance), and the conditions for the occurrence of noise-induced Hopf bifurcations are presented.

The crucial step in the derivation on the mean-field self-consistency equations for model (1) by arbitrary values of the predator growth rate  $\beta$  is to find the formal solution of the first equation in equations (1) with Eqs. (2), (6), and parameters  $\varepsilon = J = e = 0$ . Confining ourselves to the terms proportional to  $a_0^2$  (i.e., it is assumed, that the noise amplitude is small,  $a_0 << 1$ ), we get, after averaging this formal solution over the realizations of the noise Z, the following self-consistency equations [17]:

$$\begin{bmatrix} \frac{d}{dt} + v + c\gamma x^{c} - (c+1)\frac{\dot{x}}{x} \end{bmatrix} \cdot \begin{bmatrix} \frac{d}{dt} + 2\gamma cx^{c} - (c-1)\frac{\dot{x}}{x} \end{bmatrix}$$

$$(12) \quad \cdot \begin{bmatrix} \dot{x} - x + \gamma x^{c+1} + yg(x, y) \end{bmatrix}$$

$$-c^{3}\gamma^{2}(1+c)a_{0}^{2}x^{2c}(\dot{x} + \gamma x^{c+1}) = 0,$$

$$\frac{dy}{dt} = y \begin{bmatrix} \frac{\beta}{\alpha}g(x, y) - d \end{bmatrix}$$

where  $x = \langle X(t) \rangle$ ,  $\gamma = K^{-c} \{1 + a_0^2(1 + c) \cdot (c/2)\}$ , and  $\dot{x} = (dx/dt)$ . The equations (12) become a four-dimensional dynamical system of *x*,  $\dot{x}$ ,  $\ddot{x}$  and *y*. A standard linear stability analysis performed at the equilibrium point yield the conditions for the occurrence of Hopf bifurcations [17].

The results of [17] demonstrate that the functional dependence of the critical capturing rate for Hopf bifurcations  $\alpha_{cr}$  on the noise correlation time  $\tau_c$  exhibits a resonance form as  $\tau_c$  is varied. The typical forms of the graph of  $\alpha_{cr}(\tau_c)$  are represented in Fig. 4. At the condition

$$(13) d < \beta < 1 + d$$

(

one has to discern two cases. First, if  $(\beta - d) \cdot (c\beta + d) < 2c\beta \cdot (1 + d - \beta)$ , then the function  $\alpha_{cr}(\tau_c)$  has a minimum  $\alpha_{cr1}$  at a certain value  $\tau_{cm}$  of the noise correlation time  $\tau_c$ . At a long correlation time limit,  $\tau_c \rightarrow \infty$ , and also in the fast-noise limit,  $\tau_c \rightarrow 0$ , the critical capturing rate  $\alpha_{cr}$  saturates at the value

(14) 
$$\alpha_{cr0} = \frac{b\beta [c\beta + d(\beta - d)]}{(\beta - d)(c\beta + d)}$$

which corresponds to the critical capturing rate in the absence of noise. Second, in the case of  $(\beta - d) \cdot (c\beta + d) > 2c\beta (1 + d - \beta)$ , there are always two extrema of  $\alpha_{cr}(\tau_c)$ . For decreasing values of  $\tau_c$ , the critical capturing rate starts from the value determined by Eq. (14), increasing to a local maximum  $\alpha_{cr2}$ , next it decreases,



**Fig. 4.** Dependence of the critical capturing rate  $\alpha_{cr}$ ,  $\Delta \alpha_{cr} = \alpha_{cr} - \alpha_{cr_0}$ , on the noise correlation time  $\tau_c$ . System parameters: the noise variance  $a_0^2 = 0.01$ , c = 1, b = 1,  $J = e = \varepsilon = 0$ ;  $\alpha_{cr_0}$  is computed from Eq. (8). (a) The case of  $(\beta - d) \cdot (c\beta + d) < 2c\beta (1 + d - \beta)$ ; d = 0.6 and  $\beta = 0.8$ . (b) The case of  $(\beta - d) \cdot (c\beta + d) \cdot (c\beta + d) > 2c\beta \cdot (1 + d - \beta)$ ; d = 0.09 and  $\beta = 0.9$ .

attaining a local minimum  $\alpha_{cr_3}$ , and then  $\alpha_{cr}$  approaches  $\alpha_{cr_0}$  as  $\tau_c \rightarrow 0$  (see Fig. 4(b)).

Relying on Fig. 4, one can find the necessary and sufficient conditions for the emergence of a Hopf bifurcation (and re-entrant transition) due to the noise correlation time variations. For example, in the case of  $(\beta - d) \cdot (c\beta + d) > 2c\beta \cdot (1 + d - \beta), \alpha_{cr1} < \alpha < \alpha_{cr0}$  the transitions are characterized by the following scenario. For large values of the correlation time,  $\tau_c > \tau_{c1}$ , where  $\alpha < \alpha_{cr}(\tau_c)$  the system is in a stable equilibrium state  $(\langle X \rangle_s, y_s)$ . At  $\tau_c = \tau_{c1}$ , i.e.,  $\alpha = \alpha_{cr}(\tau_{c1})$ , the equilibrium point  $(\langle X \rangle_s, y_s)$  becomes locally unstable and the system exhibits a Hopf bifurcation near ( $\langle X \rangle_s, y_s$ ). Inside the interval  $\tau_{c_2} < \tau_c < \tau_{c_1}$  of the correlation time, there appears a limit cycle around  $(\langle X \rangle_s, y_s)$ , where both the predator-population and average prey-population densities oscillate. At  $\tau_c = \tau_{c_2}$ , where  $\alpha = \alpha_{cr}(\tau_{c_2})$ , the limit cycle disappears and the system approaches a new stable equilibrium state, thus making a re-entrant transition. A further decrease of  $\tau_c < \tau_{c2}$  causes just a monotonic decrease of the equilibrium state parameters  $\langle X \rangle_s$  and  $y_s$ .

The result that the fluctuations of the carrying capacities of preys can induce Hopf bifurcation and re-entrant transitions is somewhat surprising, because in the corresponding deterministic models (noise absent), the critical prey capturing rate  $\alpha_{cr}$  as well as the asymptotic behaviour of the system solutions are independent of the carrying capacity K.

#### Noise-induced relaxation oscillations

Ratio-dependent predator-prey systems

The work [17] is based on local stability analysis with the assumption that the noise dispersion (or amplitude)

is very small. As a consequence, for the emergence of the phenomenon of noise-induced Hopf bifurcation the control parameter (prey capturing rate  $\alpha$ ) must be located very near the bifurcation point  $\alpha_{cr}$  of the corresponding deterministic model. Moreover, in the case considered in [17] the trivial equilibrium ( $\langle X \rangle = 0$ , y = 0) has its own basin of attraction, even if there exists a nontrivial stable or unstable (with a stable limit cycle) equilibrium. Hence, the appearance of noise-induced Hopf bifurcation is very sensitive to small variations of the system parameters and initial conditions, and so, the results of [17] are mainly of a theoretical interest, while applications in nature seem impossible. Thus, [17] leaves as unsettled the fundamental question in the ecological context, both from the theoretical and practical viewpoints, whether environmental coloured fluctuations with a finite amplitude can cause globally asymptotically stable limit cycles in ratio-dependent predator-prey systems (or in more general systems with the Beddington functional response). The question is addressed in the papers [20, 21] and the answer is affirmative, which is a crucial result, allowing in practice to link transitions between an oscillatory regime and an equilibrium state of population sizes observed in nature with changes of environmental fluctuations.

The main contribution of the mentioned papers is as follows. In predator-prey systems (model (1) with  $\varepsilon = J = e = 0$ ), in which the growth rate of the predator population is much smaller than the growth rates of the prey,  $\beta << 1$ , we establish coloured-noise-induced transitions from a globally stable equilibrium to the stable limit cycle (with some relaxation oscillations of the population abundances) as well as in the opposite direction. Furthermore, the transitions are found to be re-entrant, e.g., if the noise amplitude is greater than a threshold value then the limit cycle appears above a critical value of the noise correlation time, but disappears again through re-entrant transition to the equilibrium state at a higher value of the correlation time.

We would like to emphasize that the works [20, 21] are addressed to that region of the system parameters where the deterministic counterpart of the model is characterized by a nontrivial globally stable equilibrium, whereas our previous work [17] examined another parameters region, where Hopf bifurcations in the corresponding deterministic model are possible. Our results indicate that the effect of noise is not merely restricted to shifts of the critical capturing rate  $\alpha_{cr}$  for Hopf bifurcations as in the case described in [17], but it will change the whole nature of the dynamics. Notably, transitions from an equilibrium state to a limit cycle are possible only if the noise amplitude is greater than a certain critical value  $a_c(\alpha)$  the critical noise amplitude  $a_{c}(\alpha)$  decreases monotonically from one to zero if the capturing rate  $\alpha$  increases up to the value b.

#### The model with the Beddington functional response

We will now consider, in brief, some aspects of the dynamics of a more general model with the Beddington functional response (model (1) with  $\varepsilon = J = 0$ ). The detailed description of the analytic results, obtained by a dynamical mean-field approximation in combination



**Fig. 5.**  $(\tau_c, a_0^2)$  phase diagram for the existence of limit cycles. The parameter values  $J = \varepsilon = 0$ ,  $\alpha = 1.05b$ , K = 21.115e,  $\beta = 0.01$ , c = 1 and d = 0.005 are used. The shaded regions correspond to the two domains, (1) and (2), where oscillations are possible. The dashed line depicts the upper border below which the relaxation oscillations are possible. More details are in the text.

with the assumption that  $\beta << 1$  is given in [18]. Our major result is the establishing of the effect of multiple transitions (more than two) between relaxation oscillatory regimes and equilibrium states, vs. noise correlation time. Figure 5 shows a phase diagram in the  $\tau_c - a_0^2$ plane at  $\alpha = 1.05b$ , K = 21.115e,  $\beta = 0.01$ , c = 1 and d = 0.005. The interesting peculiarity of the diagram is that there are two disconnected regions (the shaded areas in Fig. 5) where the limit cycle can appear. The lower domain (1) corresponds to purely noise-induced relaxation oscillations. In the larger shaded region (2) the oscillations are related to noise-influenced "deterministic" limit cycles. Here we would like to note that the corresponding deterministic model (noise absent) with conditions  $\alpha > b$  and  $K > e\alpha/(\alpha - b)$  can include a globally asymptotically stable limit cycle.

It is noteworthy that there is a critical value of the noise amplitude  $a_1$  (in Fig. 5  $a_1^2 = 0.00545$ ):

(15) 
$$a_1^2 = 1 - \frac{\alpha e}{K(\alpha - b)}, \quad \alpha > b, \quad K(\alpha - b) > \alpha e$$

below which oscillations (but not relaxation oscillations) can appear at all values of the noise correlation time. When  $\alpha_0 > \alpha_1$ , the influence of the noise is thought to be a stabilizing factor, because an increase of the noise amplitude reduces rapidly the values of the correlation time  $\tau_c$  where oscillations are possible. An important observation in domain (2) is that relaxation oscillations occur only in the relatively small wedge-shaped area (the upper border of this region is indicated with the dashed line in Fig. 5). In the case of other possible oscillations in domain (2) the slow-fast (relaxation) approach considered is invalid at low values of prey densities  $X_i$ where the dynamics of  $X_i$  is slower than that of predator density y (see also Eqs. set (1)). Moreover, in the last case, under the condition  $\beta << 1$  the cycle dynamics can come very close to the axes ( $\langle X \rangle = 0, y = 0$ ), and extinction may occur in nature due to demographic or environmental stochasticity (even if we have a stable cycle mathematically). Generally, environmental fluctuations prevent such oscillations (extinction), but the critical noise amplitude  $a_1$ , above which prevention is considerable, increases relatively rapidly as the saturation parameter *e* decreases (Eq. (15)).

#### Conclusions

We have presented some results for the mean-field dynamics of N-species stochastic Lotka-Volterra systems subjected to dichotomous noise. A major virtue of the proposed model is that interplay of coloured noise and interaction intensities of species can generate a rich variety of non-equilibrium cooperation effects, such as discontinuous non-equilibrium phase transitions and noise-induced stable limit cycles, even if the system is monostable in the absence of noise. Furthermore, our earlier results [12, 16, 22] about the dynamics of overdamped particles in a periodic, one-dimensional potential landscape subjected to a static tilting force and to both thermal noise and a non-equilibrium three-level coloured noise, show that mutual interplay of coloured and thermal noises in tilted ratchets with simple periodic potentials can induce unexpected anomalous transport phenomena. In particular, it is shown in [12, 16, 22] that such a model can exhibit hypersensitive transport, four current reversals, negative differential resistance, hypersensitive differential response, the phenomenon of disjunct "windows" for an external force, and absolute negative mobility.

As the non-equilibrium phenomena considered in this paper and in [12, 16, 22] are robust enough to survive a modification of the coloured noise as well as the prey functional response (the potential landscape in the model of [12]), the results of the investigations of the basic models (model (1) and the model of Ref. [12]) can be applied for a variety of purposes. Possible applications range along from ecosystems [14, 17–21, 25, 27] to intracellular protein transport in biology, or to methods of particle separation in nanotechnology [13, 24].

We believe that both the above described model and the model represented in [12] may also shed some light on the stochastic interaction processes of plasma with wall materials in plasma focus devices and will give some hints for the elaboration of realistic physical models for non-equilibrium transport and phase transitions by such interaction processes. The idea is that the particles of the surface, like predators, "consume" the hot plasma particles ("prey") while gradually changing their own quality. This resembance should but be modelled by a certain correspondence of the stochastic parameters.

Finally, we point out that although model (1) is not immediately applicable in the context of plasma focus devices, our exact analytical results can form a good starting point for the investigation of more realistic models. Probably, model (1) can be expanded, along the lines described in [2, 3, 5, 7], where the formation of noise-induced spatiotemporal structures in gasdischarge systems is considered both experimentally and theoretically, into one that is suitable for studying pattern formation by plasma beam interactions with construction materials. In particular, the mathematical structure of the spatially discrete version of the model considered in [2, 3] is somewhat similar to the structure of Eqs. (1) with Eqs. (2) and (6) (the voltage drop and density of charge carriers in a discharge gap correspond to a prey and a predator, respectively).

Acknowledgment. This work was partly supported by the International Atomic Energy Agency Grant no. 12062 and the Estonian Science Foundation Grants nos. 7319 and 7048.

#### References

- Arditi R, Ginzburg LR (1989) Coupling in consumerresource dynamics: ratio-dependence. J Theoret Biol 139:311–326
- Astrov YuA, Fradkov AL, Guzenko PYu (2008) Control of a noise-induced transition in a nonlinear dynamical system. Phys Rev E 77:026201
- Astrov YuA, Logvin YuA (1997) Formation of clusters of localized states in a gas discharge system via a selfcompletion scenario. Phys Rev Lett 79:2983–2986
- Beddington JR (1975) Mutual interference between parasites or predators and its effect on searching efficiency. J Anim Ecol 44:331–340
- Benilov MS (2008) Bifurcations of current transfer through a collisional sheath with ionization and selforganization of glow cathodes. Phys Rev E 77:036408
- 6. Berryman A (2002) Population cycles: the case for trophic interactions. Oxford University Press, Oxford
- Bödeker HU, Röttger MC, Liehr AW, Frank TD, Friedrich R, Purwins H-G (2003) Noise-covered drift bifurcation of dissipative solitons in a planar gas-discharge system. Phys Rev E 67:056220
- 8. Ciuchi S, de Pasquale F, Spagnolo B (1996) Self-regulation mechanism of an ecosystem in a non-Gaussian fluctuation regime. Phys Rev E 54:706–716
- 9. Gammaitoni L, Hänggi P, Jung P, Marchesoni F (1998) Stochastic resonance. Rev Mod Phys 70:223–287
- 10. García-Ojalvo J, Sancho JM (1999) Noise in spatially extended systems. Springer-Verlag, New York
- 11. Horsthemke W, Lefever R (1984) Noise-induced transitions. Springer-Verlag, New York
- Laas T, Sauga A, Mankin R, Ainsaar A, Ugaste Ü, Rekker A (2006) Colored-noise-induced anomalous transport in periodic structures. Nukleonika 51;1:63–69

- Linke H (ed) (2002) Special issue on "Ratchets and Brownian motors: basics, experiments and applications". Appl Phys A 75:167–352
- Mankin R, Ainsaar A, Haljas A, Reiter E (2002) Trichotomous-noise-induced catastrophic shifts in symbiotic ecosystems. Phys Rev E 65:051108
- 15. Mankin R, Ainsaar A, Reiter E (1999) Trichotomous noise-induced transitions. Phys Rev E 60:1374–1380
- Mankin R, Haljas A, Tammelo R, Martila D (2003) Mechanism of hypersensitive transport in tilted sharp ratchets. Phys Rev E 68:011105
- Mankin R, Laas T, Sauga A, Ainsaar A, Reiter E (2006) Colored-noise-induced Hopf bifurcations in predatorprey communities. Phys Rev E 74:021101
- Mankin R, Laas T, Soika E, Ainsaar A (2007) Noisecontrolled slow-fast oscillations in predator-prey models with the Beddington functional response. Eur Phys J B 59:259–269
- Mankin R, Sauga A, Ainsaar A, Haljas A, Paunel K (2004) Colored-noise-induced discontinuous transitions in symbiotic ecosystems. Phys Rev E 69:061106
- Mankin R, Sauga A, Laas T, Soika E (2007) Environmental-fluctuations-induced slow-fast cycles in ratiodependent predator-prey systems. WSEAS Transactions on Systems 6:934–941
- 21. Mankin R, Sauga A, Laas T, Soika E (2007) Noisecontrolled relaxation oscillations in ratio-dependent predator-prey models. In: Proc of the 3rd WSEAS Int Conf on Mathematical Biology and Ecology, 17–19 January 2007, Gold Coast, Australia, 1:12–20
- Martila D, Mankin R, Tammelo R, Sauga A, Reiter E (2006) Constructive influence of noise-flatness in correlation ratchets. Eur Phys J B 54:375–383
- Pimenov VN, Gribkov VA, Dubrovsky AV et al. (2002) Influence of powerful pulses of hydrogen plasma upon materials in PF-1000 device. Nukleonika 47;4:155–162
- 24. Reimann P (2002) Brownian motors: noisy transport far from equilibrium. Phys Rep 361:57–265
- Sauga A, Mankin R (2005) Addendum to colored-noiseinduced discontinuous transitions in symbiotic ecosystems. Phys Rev E 71:062103
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596
- 27. Spagnolo B, Valenti D, Fiasconaro A (2004) Noise in ecosystems: a short review. Math Biosci Eng 1:185–211