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Role of noise in population dynamics cycles

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Noise is an intrinsic feature of population dynamics and plays a crucial role in oscillations called phase-forgetting quasicycles by converting damped into sustained oscillations. This function of noise becomes evident when considering Langevin equations whose deterministic part yields only damped oscillations. We formulate here a consistent and systematic approach to population dynamics, leading to a Fokker-Planck equation and the associate Langevin equations in accordance with this conceptual framework, founded on stochastic lattice-gas models that describe spatially structured predator-prey systems. Langevin equations in the population densities and predator-prey pair density are derived in two stages. First, a birth-and-death stochastic process in the space of prey and predator numbers and predator-prey pair number is obtained by a contraction method that reduces the degrees of freedom. Second, a van Kampen expansion in the inverse of system size is then performed to get the Fokker-Planck equation. We also study the time correlation function, the asymptotic behavior of which is used to characterize the transition from the cyclic coexistence of species to the ordinary coexistence.

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I. INTRODUCTION

Random fluctuations are an inherent feature observed in populations of biological species [1,2]. The number of species individuals fluctuates in time and space. In particular, fluctuations are observed in populations exhibiting time oscillations such as those of a predator-prey system [1–7]. In this context, an important question arises concerning the role of noise in a biological system exhibiting cycles. Naively one might imagine that noise would destroy oscillations. Actually, in some circumstances quite the contrary happens. Without noise the oscillations are in fact absent, or at most they are damped oscillations. The noise plays then a crucial role by converting the damped into undamped oscillations. Of course, noise by itself would not produce cycles. There must be an underlying mechanism resulting from the predator-prey interactions that yields damped oscillations in the absence of noise.

This conceptual framework has been conjectured by Bartlett [8] and advanced by Nisbet and Gurney [9]. However, a precise explanation for the existence of undamped oscillations was given only more recently by McKane and Newman [10] by means of a birth-and-death stochastic predator-prey model. By deriving Langevin equations from this stochastic predator-prey model, these authors showed that predator and prey numbers exhibit oscillations that emerge from a resonance effect and vanish when one takes the limit of infinite number of individuals. The set of differential equations made up of the deterministic part of the Langevin equations is such that it predicts only damped oscillations. The noise part converts the damped into undamped oscillations. These ideas were subsequently extended by Lugo and McKane [11] by means of stochastic spatial models where each site of a lattice, representing a patch, can have many individuals of either species. The derivation of Langevin equations from stochastic models has also been carried out by other authors [12,13].

Stochastic models that have been used to study predator-prey systems may or may not take into account the spatial structure of the habitat. The nonspatial models usually are one-step processes or zero-dimensional stochastic processes called birth-and-death processes [1,2,14,15] described by few stochastic variables, namely, the numbers of individuals of each species [10,16–19]. The spatial models can be arranged into at least two classes. One class [11,20] encompasses those stochastic lattice models for which the habitat is described by a lattice of sites, each site representing a patch with many individuals. The other class [21–36] comprises the stochastic lattice-gas models, also called interacting particle systems [37,38], for which the habitat is also represented by a lattice of sites but each site can be occupied by at most one individual (multiple occupancy is not allowed) describing the discreteness of individuals. These models are continuous time Markov processes described by a set of discrete stochastic variables, representing the species individuals, residing on the sites of a finite lattice of N sites.

The purpose of this paper is to show that Langevin equations exhibiting properties in accordance with the framework mentioned above can also be derived from predator-prey stochastic lattice-gas models [21–36]. Here we focus on a predator-prey stochastic lattice-gas model introduced by Satulovsky and Tomé [22] but the approach is general. The derivation is performed in two stages. In the first stage we obtain a birth-and-death master equation describing a stochastic dynamics in the space of population numbers. In the second stage, the Fokker-Planck equation and the associate Langevin equations are obtained from the birth-and-death master equation by a $1/N$ expansion [1,2,39], of the type put forward by van Kampen [14,15]. The expansion we use is distinct from that used by Lugo and McKane [11] in the following sense. These authors use an expansion in the inverse of the carrying capacity (maximum number of individuals in a site). Such an expansion cannot be applied to stochastic lattice-gas models because site occupancy is restricted to few particles. We instead make an expansion in the inverse of the system size.

The birth-and-death master equation is here derived from the stochastic lattice-gas models by the use of a contraction method leading to the reduction in the number of degrees of freedom. This reduction is carried out in two ways. In the first, the resulting stochastic process described by the birth-and-death master equation involves the prey and predator numbers only. In the second, it involves in addition the number of neighboring predator-prey pairs. The reduction method we use leads to a continuous description of the predator-prey system and differs from the method devised by Mobilia *et al.* [33] who use the Doi-Peliti formalism to derive from the lattice-gas model a continuous field theoretic description for a predator-prey system.

The $1/N$ expansion, as we shall see, implies that the amplitude of the undamped oscillations in the population number increases as $\sqrt{N}$, or equivalently the amplitude in the population density decreases as $1/\sqrt{N}$, a property that has been observed in the stochastic lattice-gas model studied here [22] and also in other stochastic lattice-gas models [24–26]. Oscillations in lattice models with this property are identified as local oscillations [22,24–26] in contrast to global oscillations for which the amplitude of the population number increases as N so that the amplitude of the population density remains the same.

The important property that the amplitude of the oscillations increases as $\sqrt{N}$ cannot alone be used to distinguish oscillations from fluctuations because the size of stochastic fluctuations also increases as $\sqrt{N}$. The proper way to distinguish between them is by means of the time correlation function. Ordinary stochastic fluctuations have time correlation functions that decay exponentially with time charactering ordinary Brownian noise. Undamped local oscillations, also called phase-forgetting quasicycles [1,2], have time correlation functions exhibiting damped oscillations (asymptotically a damped sinusoidal function), which we call chromatic Brownian noise. We remark that global oscillations, not seen in the present study, and also called phase-remembering quasicycles [1,2], have time correlation functions that are asymptotically pure sinusoidal.

The aim of this paper is also to characterize the transition from oscillatory behavior to ordinary behavior, without oscillations. This can be done by considering the dominant eigenvalue of the Jacobian matrix associated to the deterministic part of the Langevin equations. The dominant eigenvalue determines the asymptotic behavior of the time correlation functions. If it is real then the time correlation function decays exponentially characterizing an ordinary noncyclic behavior. If it is complex than the time correlation function is a sinusoidal exponentially decaying function characterizing the undamped cyclic behavior or phase-forgetting quasicycles. The imaginary part of the complex eigenvalue is identified as the frequency of oscillations. A transition from one type of behavior to the other may be defined as the point where the real eigenvalue equals the real part of the complex eigenvalue. The imaginary part of the dominant eigenvalue may be considered as an order parameter. Notice that while this is not a phase transition in the thermodynamic sense, it is however a real change in the behavior of populations that can actually be observed.

It is worth mentioning that the stochastic lattice-gas models and the birth-and-death stochastic processes are approaches representing two distinct levels of stochastic description in population dynamics. The former corresponds to a microscopic description in which the spatial structure is explicitly taken into account and each individual is represented by a stochastic variable. The latter corresponds to a mesoscopic or a coarse grained description in which the spatial structure is neglected and the species individuals are described collectively by their numbers that work as stochastic variables. There is also a third level of description represented by the deterministic ordinary differential equations in which noise and the spatial structure are absent and regarded as mean-field-type theories.

II. STOCHASTIC LATTICE-GAS MODEL

The stochastic lattice-gas model [22] that we consider here consists of three subprocesses: (a) the autocatalytic creation of prey, (b) the catalytic creation of a predator and simultaneous annihilation of prey, and (c) spontaneous annihilation of predators. At each site i of a square lattice there is a stochastic variable η_i that takes the value 0, 1, or 2, according to whether the site i is empty, occupied by a prey individual, or occupied by a predator. For convenience we use projector variables p_i, n_i, and m_i that take the values 0 or 1. If site i is empty, $p_i=1$, otherwise, $p_i=0$; if it is occupied by a prey individual, $n_i=1$, otherwise, $n_i=0$; and if it is occupied by a predator, $m_i=1$, otherwise, $m_i=0$. They are related by $p_i+n_i+m_i=1$ and satisfy the projection relations $p_i^2=p_i$, $n_i^2=n_i$, $m_i^2=m_i$ and $p_in_i=n_im_i=p_im_i=0$. The transitions allowed are those in which the state of a site changes in the cycle order $0\to1\to2\to0$. The corresponding transition rate $w_i(\eta)$ is given by

$$w_i(\eta)=\frac{a}{4}p_i\sum_\delta n_{i+\delta}+\frac{b}{4}n_i\sum_\delta m_{i+\delta}+cm_i, \tag{1}$$

where the summations are performed over the nearest neighbor of site i and a, b, and c are parameters related to the creation of prey, creation of a predator, and annihilation of predators, respectively.

The time evolution of the probability distribution $P(\eta,t)$ at time t of a configuration $\eta=\{\eta_i\}$ is governed by the master equation

$$\frac{d}{dt}P(\eta,t)=\sum_i\{w_i(\eta^i)P(\eta^i,t)-w_i(\eta)P(\eta)\}, \tag{2}$$

where the state denoted by η^i is obtained from η by an anticyclic permutation of the state of site i, that is, $2\to1\to0\to2$. By rescaling time we may assume that $a+b+c=1$, with $0\le a,b,c\le1$.

For later use we define the variables $n=\Sigma_in_i$ as the prey number, $m=\Sigma_im_i$ as the predator number, and $p=\Sigma_ip_i$ as the number of empty sites. They are related by $n+m+p=N$, where N is the number of sites of the lattice. We define also the variables $x=n/N$, the prey density, $y=m/N$, the predator density, and $z=p/N$, the density of empty sites. They are related by $x+y+z=1$.

III. BIRTH-AND-DEATH STOCHASTIC PROCESS

We start by writing a master equation for the birth-and-death stochastic process, which gives the time evolution of the joint probability $P(n,m,t)$ of the system having n prey individuals and m predators. The most general form for a one-step master equation is

$$\frac{d}{dt}P(n,m,t)=N\sum_{\sigma=-1}^{+1}\sum_{\tau=-1}^{+1}\{A_{\sigma\tau}(n-\sigma,m-\tau)P(n-\sigma,m-\tau,t)-A_{\sigma\tau}(n,m)P(n,m,t)\}, \tag{3}$$

where $A_{\sigma\tau}(n,m)$ is the rate of the transition $(n,m)\rightarrow(n+\sigma,m+\tau)$, where the increments σ and τ can be $0,\pm 1$. This equation is obtained directly from the master Eq. (2) by writing $P(n,m,t)$ in place of $P(\eta,t)$, a procedure that results in the following relations between the transitions rates $A_{\sigma\tau}$ and the microscopic transition rate w_i,

$$A_{+0}=\langle\langle p_i w_i\rangle\rangle=au, \tag{4}$$

$$A_{-+}=\langle\langle n_i w_i\rangle\rangle=bv, \tag{5}$$

$$A_{0-}=\langle\langle m_i w_i\rangle\rangle=cy, \tag{6}$$

where the notation $\langle\langle f_i\rangle\rangle$ does not mean an average in probability but merely stands for $(1/N)\Sigma_i f_i$. The quantities u and v are defined by

$$u=\frac{1}{4}\sum_{\delta}\langle\langle p_i n_{i+\delta}\rangle\rangle, \quad v=\frac{1}{4}\sum_{\delta}\langle\langle n_i m_{i+\delta}\rangle\rangle \tag{7}$$

and are the density of prey individuals next to an empty site and the density of predators next to a prey individual, respectively. The other transition rates vanish.

As it stands Eq. (3) is not a closed equation for $P(n,m,t)$ and thus not a proper master equation because the transitions A_{+0} and A_{-+} are not yet known functions of n and m. If, however, one uses an approximation analogous to that used in the simple mean-field approximation, namely, $\langle\langle p_i n_j\rangle\rangle=\langle\langle p_i\rangle\rangle\langle\langle n_j\rangle\rangle$ and $\langle\langle n_i m_j\rangle\rangle=\langle\langle n_i\rangle\rangle\langle\langle m_j\rangle\rangle$, that is, $u=zx$ and $v=xy$, then

$$A_{+0}=azx, \tag{8}$$

and

$$A_{-+}=bxy. \tag{9}$$

Since $x=n/N$ and $y=m/N$ and $z=1-x-y$, the transition rates $A_{\sigma\tau}$ are now functions or n and m and Eq. (3) becomes a genuine master equation for $P(n,m)$. Another equivalent way of reaching Eqs. (3), (6), (8), and (9) is presented in the Appendix. We remark that it is also possible to formulate the truncation scheme in a local version [32,40].

The birth-and-death stochastic process defined by Eq. (3) can be regarded as a random walk in the space (n,m) as demonstrated in Fig. 1 where the possible jumps are represented by arrows. The allowed jumps are (a) $(n,m)\rightarrow(n+1,m)$, with probability A_{+0}, (b) $(n,m)\rightarrow(n-1,m+1)$, with probability A_{-+}, and (c) $(n,m)\rightarrow(n,m-1)$ with probability A_{0-}. Notice the presence of two absorbing states. One of them is $(n,m)=(0,0)$ corresponding to the extinction of both species, which however is unstable and never occurs. The other is $(n,m)=(N,0)$ corresponding to prey repletion and occurs at sufficient large values of c.

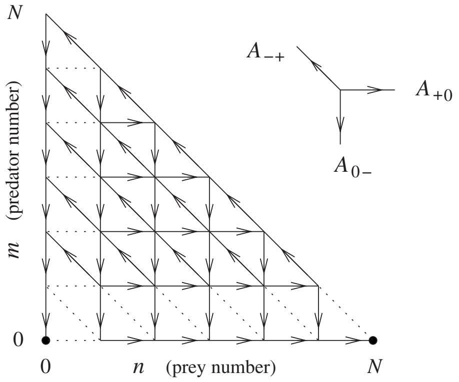

FIG. 1. Transitions of the birth-and-death stochastic process in the space of prey and predator numbers. The transition to the east represents a prey birth with rate A_{+0}, to the northwest a prey death and a simultaneous predator birth with rate A_{-+}, to the south a predator death with rate A_{0-}. The full circles represent absorbing states.

IV. LANGEVIN EQUATIONS

When N is large we may consider the expansion of the master Eq. (3) in powers of $1/N$. We use an expansion technique based on a Taylor expansion that has been used successfully to reduce birth-and-death master equation to a Fokker-Planck equation [1,2,39]. In the large N regime the quantities $x=n/N$ and $y=m/N$ become quasicontinuous variables that allow us to introduce the probability density $\mathcal{P}(x,y,t)$, related to the probability distribution $P(n,m)$ by $\mathcal{P}(x,y,t)=N^2P(n,m,t)$. From Eqs. (6), (8), and (9), the quantities $A_{\sigma\tau}(n,m)=\mathcal{A}_{\sigma\tau}(x,y)$ are actually functions of x and y. Therefore the first term inside the curly brackets in Eq. (3) can be written as $\mathcal{A}_{\sigma\tau}(x-\sigma/N,y-\tau/N)\mathcal{P}(x-\sigma/N,y-\tau/N,t)$. A Taylor expansion of this term up to second order in $1/N$ leads us to the following Fokker-Planck for the probability density $\mathcal{P}(x,y,t)$,

$$\frac{\partial}{\partial t}\mathcal{P}=-\frac{\partial}{\partial x}(f_1\mathcal{P})-\frac{\partial}{\partial y}(f_2\mathcal{P})+\frac{1}{2N}\left[\frac{\partial^2}{\partial x^2}(D_{11}\mathcal{P})+2\frac{\partial^2}{\partial x\,\partial y}(D_{12}\mathcal{P})+\frac{\partial^2}{\partial y^2}(D_{22}\mathcal{P})\right], \tag{10}$$

where

$$f_1(x,y)=azx-bxy, \quad f_2(x,y)=bxy-cy, \tag{11}$$

and

$$D_{11}(x,y)=azx+bxy, \quad D_{12}(x,y)=-bxy, \tag{12}$$

$$D_{22}(x,y)=bxy+cy.$$

This Fokker-Planck equation is equivalent to the following Langevin equations:

$$\frac{dx}{dt}=f_1(x,y)+\frac{1}{\sqrt{N}}\xi_1(t), \tag{13}$$

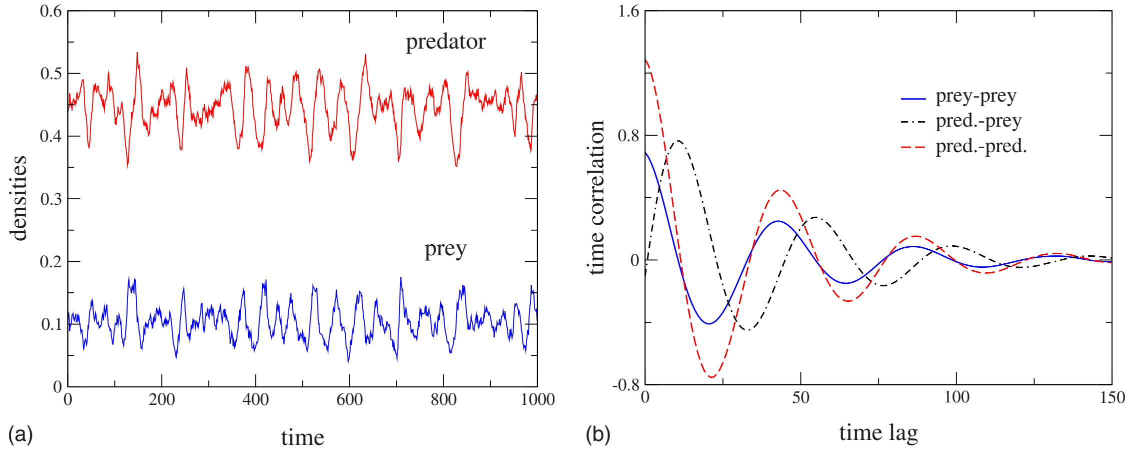

FIG. 2. (Color online) Simulations of the birth-and-death stochastic process for the case $a=b=0.475$ and $c=0.05$ and $N=1000$ showing oscillations of the type phase-forgetting quasicycles. (a) Prey and predator densities as functions of time (with arbitrary origin). (b) Time correlation functions against time lag.

$$\frac{dy}{dt} = f_2(x,y) + \frac{1}{\sqrt{N}}\xi_2(t), \qquad (14)$$

where $\xi_i(t)$, with $i=1,2$, are white Gaussian noise functions with zero mean obeying the properties

$$\langle \xi_i(t)\xi_j(t')\rangle = D_{ij}(x,y)\delta(t-t'). \qquad (15)$$

The second term on the right-hand side of Eqs. (13) and (14), the noise term, decreases as $1/\sqrt{N}$ so that the amplitude of the noisy oscillations in the densities x and y, illustrated in Fig. 2, decrease also as $1/\sqrt{N}$.

The Langevin equations can be simulated by standard procedures. Since for sufficiently large N they are equivalent to the birth-and-death process defined by the master Eq. (3) we may instead simulate the birth-and-death process. An example of phase-forgetting quasicycles and the respective correlation functions obtained from numerical simulations of the birth-and-death process, defined by the master Eq. (3), is shown in Fig. 2.

Let us analyze Eqs. (13) and (14) for large times. Without noise, the densities x and y approach their asymptotic values x^* and y^* given by $f_1(x^*,y^*)=0$ and $f_2(x^*,y^*)=0$, which yields

$$x^* = c/b, \quad y^* = a(b-c)/b(a+b), \qquad (16)$$

valid as long as $c<b$, corresponding to a state where the species coexist. Other solutions are $(x^*,y^*)=(1,0)$, corresponding to a prey absorbing state, and $(x^*,y^*)=(0,0)$, corresponding to empty absorbing state or the extinction of both species.

The stability of the three types of solutions can be inferred from the eigenvalues of the Jacobian matrix J calculated at the fixed point (x^*,y^*) given by

$$J = \begin{pmatrix} az^* - ax^* - by^* & -ax^* - bx^* \\ by^* & -c + bx^* \end{pmatrix}. \qquad (17)$$

When $(x^*,y^*)=(0,0)$, the eigenvalues are a and $-c$ so that this solution is always unstable. The eigenvalues corresponding to the prey absorbing state, $(x^*,y^*)=(1,0)$, are $-a$ and $b-c$ so that it is stable as long as $b<c$.

Species coexistence, occurring when $c<b$, is associated to the fixed point given by Eq. (16) and to the following Jacobian:

$$J = \begin{pmatrix} -ac/b & -(a+b)c/b \\ a(b-c)/(a+b) & 0 \end{pmatrix}. \qquad (18)$$

In this case the eigenvalues are the roots of the equation $b\lambda^2 + ac\lambda + ac(b-c)=0$. If $ac>4b(b-c)$ the eigenvalues are real and negative and the fixed point (x^*,y^*) is a node. Otherwise, the eigenvalues are complex and the fixed point is a focus. Figure 3 shows the eigenvalues as a function of the parameter c for the case $a=b$. The change in behavior, from

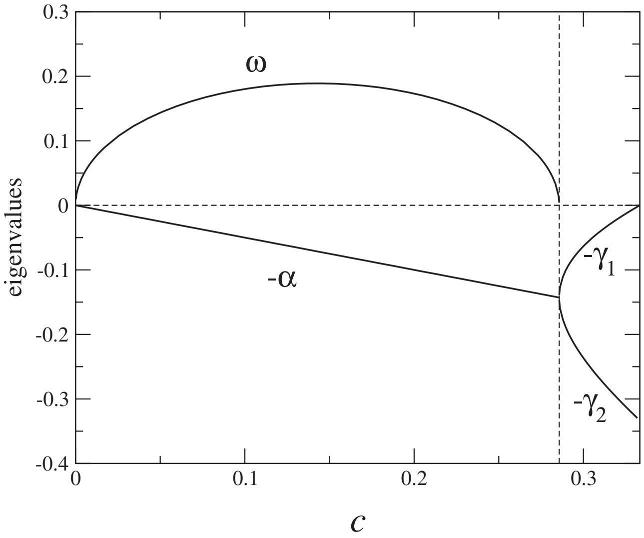

FIG. 3. Real eigenvalues ($-\gamma_1$ and $-\gamma_2$), real ($-\alpha$) and imaginary (ω) parts of the complex eigenvalue as determined by the simple mean-field approximation. The vertical dotted line at $c^*=2/7=0.2857$ indicates the transition from oscillatory to ordinary behavior.

a focus to a node, occurs when $ac=4b(b-c)$, which in the case $a=b$ occurs at $c=2/7$.

V. TIME CORRELATION FUNCTIONS

Without noise the oscillations in densities are either damped, characterized by a focus, or nonexistent, characterized by a node. To get undamped oscillations, such as the ones illustrated in Fig. 2, we have to take into account the noise, which activates the otherwise damped oscillations. One way of showing that the set of Langevin equations indeed predicts undamped oscillations is to determine the asymptotic behavior of the time correlation functions, which are obtained from a linearized form of the Langevin equations. For large values of N the noise term will be small so that, for large times, deviations of x and y from x^* and y^* will also be small. The linearization of the Langevin equations yields

$$\frac{dx}{dt} = J_{11}(x-x^*) + J_{12}(y-y^*) + \frac{1}{\sqrt{N}}\xi_1, \qquad (19)$$

$$\frac{dy}{dt} = J_{21}(x-x^*) + J_{22}(y-y^*) + \frac{1}{\sqrt{N}}\xi_2, \qquad (20)$$

where the coefficients J_{ij} are the elements of the Jacobian matrix given by Eq. (18) and the strengths of the noise are

$$D_{11} = 2D, \quad D_{12} = 2D, \quad D_{22} = -D, \qquad (21)$$

where $D=ac(b-c)/b(a+b)$.

The time autocorrelation function for prey is defined by

$$C_{11}(t) = \langle [x(t_w+t)-x^*][x(t_w)-x^*]\rangle, \qquad (22)$$

where t_w is the waiting time and t is the time lag. The time autocorrelation function for predator and the cross-correlation function are defined in a similar way. The asymptotic behavior is obtained from the linearized Langevin equations which can be exactly solved. It is straightforward to show that the solution of the linearized Langevin equations gives

$$C_{11}(t) = \frac{D}{N}(a_1 e^{\lambda_1 t} + a_2 e^{\lambda_2 t}), \qquad (23)$$

where λ_1 and λ_2 are the eigenvalues of Jacobian matrix (18). Therefore if the eigenvalues are complex, the fixed point of the deterministic part of the Langevin equation is a focus and the time correlation function is of the type

$$C_{11}(t) \sim e^{-\alpha t}\cos \omega t, \qquad (24)$$

where $-\alpha$ and ω are the real and imaginary parts of the complex eigenvalue. This correlation function characterizes the phase-forgetting quasicycles with chromatic Gaussian noise as illustrated in Fig. 2.

In the case of real eigenvalues, the fixed point of the deterministic part of the Langevin equation is a node and the asymptotic behavior is given by

$$C_{11}(t) \sim e^{-\gamma t}, \qquad (25)$$

where $-\gamma$ is the largest real eigenvalue. This describes a noncyclic ordinary species coexistence with ordinary Gaussian noise.

The eigenvalues of the Jacobian are shown in Fig. 3 as a function of the parameter c, for $a=b$ in the interval $0<c<c_c$, where $c_c=1/3$. For these values of the parameters the system is characterized by an active state where the species coexist. At $c=c_c$ there is a phase transition from an active state where the species coexist to the prey absorbing state occurring when $c_c<c$. In the interval $0<c<c^*$ where $c^*=2/7$ the two eigenvalues are complex conjugate and the system exhibits stochastic oscillations of the type phase-forgetting quasicycles with time correlation functions of type (24). In the interval $c^*<c<c_c$ where $c_c=1/3$ the eigenvalues are real and the system shows ordinary fluctuations without cycles with time correlation functions of type (25). Inside the active state there is then a transition from the oscillatory behavior to nonoscillatory behavior occurring at $c=c^*$. The imaginary part of the complex eigenvalue, identified as the frequency of oscillations and regarded as the order parameter that characterizes the oscillatory state, vanishes continuously at $c=c^*$.

VI. APPROXIMATION OF THE SECOND ORDER

The birth-and-death stochastic process in two stochastic variables obtained in Sec. III corresponds to the simplest stochastic mesoscopic description. It is possible to set up other mesoscopic descriptions with more stochastic variables. In this section we set up a mesoscopic description of the second order in which we take another stochastic variable in addition to n and m. A relevant new variable to be added is the number ℓ of nearest-neighbor pairs of predator-prey. We follow here a procedure similar to that used in the Sec. III. The joint probability $P(n,m,\ell,t)$ obeys the master equation

$$\frac{d}{dt}P(n,m,\ell,t) = N\sum_{\sigma=-1}^{+1}\sum_{\tau=-1}^{+1}\sum_{\varepsilon=-1}^{+1}\{A_{\sigma\tau\varepsilon}(n-\sigma,m-\tau,\ell-\varepsilon) \times P(n-\sigma,m-\tau,\ell-\varepsilon,t) - A_{\sigma\tau\varepsilon}(n,m,\ell)P(n,m,\ell,t)\}, \qquad (26)$$

where $A_{\sigma\tau\varepsilon}(n,m,\ell)$ are the rate of the transitions $(n,m,\ell)\to(n+\sigma,m+\tau,\ell+\varepsilon)$ where the increments σ, τ, and ε take the values $0,\pm1$. The nonzero transitions are

$$A_{+00} = \frac{1}{4}\sum_{\delta}\langle\langle (p_{i+\delta}+n_{i+\delta})p_i w_i\rangle\rangle, \qquad (27)$$

$$A_{+0+} = \frac{1}{4}\sum_{\delta}\langle\langle m_{i+\delta}p_i w_i\rangle\rangle, \qquad (28)$$

$$A_{-++} = \frac{1}{4}\sum_{\delta}\langle\langle n_{i+\delta}n_i w_i\rangle\rangle, \qquad (29)$$

$$A_{-+-} = \frac{1}{4}\sum_{\delta} \langle\langle m_{i+\delta} n_i w_i \rangle\rangle, \tag{30}$$

$$A_{-+0} = \frac{1}{4}\sum_{\delta} \langle\langle p_{i+\delta} n_i w_i \rangle\rangle, \tag{31}$$

$$A_{0--} = \frac{1}{4}\sum_{\delta} \langle\langle n_{i+\delta} m_i w_i \rangle\rangle, \tag{32}$$

$$A_{0-0} = \frac{1}{4}\sum_{\delta} \langle\langle (m_{i+\delta} + p_{i+\delta}) m_i w_i \rangle\rangle. \tag{33}$$

The master Eq. (26) is not a closed equation for $P(n,m,\ell,t)$ since the transition rates $A_{\sigma\tau\varepsilon}$ are not yet known functions of n, m, and ℓ. To get a closed equation we will use a mean-field-like approximation at the level of pair approximation.

Mean-field approximations have been used in the study of nonequilibrium stochastic lattice-gas models [22,32,40–43]. They have to do with spatial correlations between sites of the lattice and can be understood as a truncation scheme used to reduce the number of equations for the correlations. The most simple mean field is the one-site approximation in which all correlations are neglected. For instance, a two-site correlation $p(s_0,s_1)$ is written as the product $p(s_0)p(s_1)$. To get a better approximation we must include correlations at least between nearest-neighbor sites. This is done in the so-called mean-field pair approximation in the following way. Consider the conditional probability $p(s_1,s_2|s_0)$ of a given cluster of sites formed by a central site s_0 and two nearest neighbors s_1 and s_2. This conditional probability is approximated by $p(s_1,s_2|s_0)=p(s_1|s_0)p(s_2|s_0)$, which results in the following approximated probability of the cluster of sites $p(s_1,s_2,s_0)=p(s_1,s_0)p(s_2,s_0)/p(s_0)$.

Using the approximation procedure just explained a correlation of three sites such as $\langle\langle m_j n_i m_k \rangle\rangle$, where j and k are distinct nearest neighbors of site i, is written as $\langle\langle m_j n_i \rangle\rangle \langle\langle n_i m_k \rangle\rangle / \langle\langle n_i \rangle\rangle$ and two-site quantities other than $\langle\langle n_i m_j \rangle\rangle$ are approximated by the analogous of a simple mean-field approximation. This procedure leads to the results

$$A_{+00} = axz - \frac{3a}{4}xyz, \tag{34}$$

$$A_{+0+} = \frac{3a}{4}xyz, \tag{35}$$

$$A_{-++} = \frac{3b}{4}xv, \tag{36}$$

$$A_{-+-} = \frac{b}{4}v + \frac{3b}{4}\frac{v^2}{x}, \tag{37}$$

$$A_{-+0} = \frac{3b}{4}\left(v - xv - \frac{v^2}{x}\right), \tag{38}$$

$$A_{0--} = cv, \tag{39}$$

$$A_{0-0} = c(y - v). \tag{40}$$

Since $x=n/N$, $y=m/N$, and $v=\ell/N$, the rates $A_{\sigma\tau\varepsilon}$ are now functions of n, m, and ℓ and Eq. (26) becomes a genuine master equation for the probability $P(n,m,\ell,t)$.

The expansion of the master Eq. (26) in powers of $1/N$, up to first order in $1/N$, gives the following Fokker-Planck equation for the probability density $\mathcal{P}(x,y,v,t)$:

$$\begin{aligned}\frac{\partial}{\partial t}\mathcal{P} = & -\frac{\partial}{\partial x}(f_1\mathcal{P}) - \frac{\partial}{\partial y}(f_2\mathcal{P}) - \frac{\partial}{\partial v}(f_3\mathcal{P}) \\ & + \frac{1}{2N}\left[\frac{\partial^2}{\partial x^2}(D_{11}\mathcal{P}) + \frac{\partial^2}{\partial y^2}(D_{22}\mathcal{P}) + \frac{\partial^2}{\partial v^2}(D_{33}\mathcal{P})\right] \\ & + \frac{1}{N}\left[\frac{\partial^2}{\partial x\,\partial y}(D_{12}\mathcal{P}) + \frac{\partial^2}{\partial x\,\partial v}(D_{13}\mathcal{P}) + \frac{\partial^2}{\partial y\,\partial v}(D_{23}\mathcal{P})\right],\end{aligned} \tag{41}$$

where

$$f_1(x,y,v) = axz - bv, \tag{42}$$

$$f_2(x,y,v) = bv - cy, \tag{43}$$

$$f_3(x,y,v) = \frac{3}{4}\left(axyz + bxv - b\frac{v^2}{x}\right) - \left(\frac{b}{4} + c\right)v, \tag{44}$$

and

$$D_{11}(x,y,v) = axz + bv, \tag{45}$$

$$D_{22}(x,y,v) = bv + cy, \tag{46}$$

$$D_{33}(x,y,v) = \frac{3}{4}\left(axyz + bxv + b\frac{v^2}{x}\right) + \left(\frac{b}{4} + c\right)v, \tag{47}$$

$$D_{12}(x,y,v) = -bv, \tag{48}$$

$$D_{13}(x,y,v) = \frac{3}{4}\left(axyz - bxv + b\frac{v^2}{x}\right) - \frac{b}{4}v, \tag{49}$$

$$D_{23}(x,y,v) = \frac{3}{4}\left(bxv - b\frac{v^2}{x}\right) - \left(\frac{b}{4} - c\right)v. \tag{50}$$

This Fokker-Planck equation is equivalent to the following set of Langevin equations:

$$\frac{dx}{dt} = f_1(x,y,v) + \frac{1}{\sqrt{N}}\xi_1, \tag{51}$$

$$\frac{dy}{dt} = f_2(x,y,v) + \frac{1}{\sqrt{N}}\xi_2, \tag{52}$$

$$\frac{dv}{dt} = f_3(x,y,v) + \frac{1}{\sqrt{N}}\xi_3, \tag{53}$$

where $\xi_i(t)$, with $i=1$, 2, and 3, are white Gaussian noise functions with zero mean obeying the relations

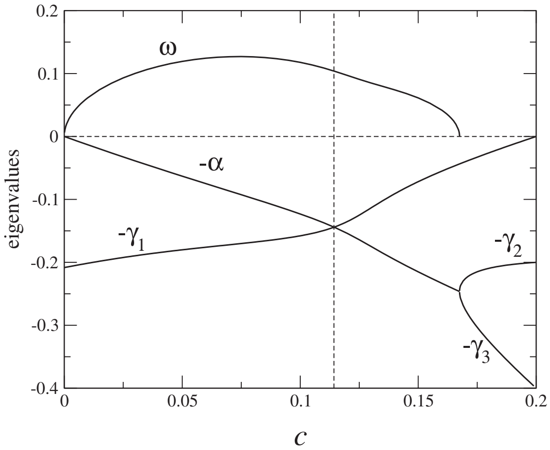

FIG. 4. Real eigenvalues ($-\gamma_1$, $-\gamma_2$, and $-\gamma_3$), real ($-\alpha$) and imaginary (ω) parts of the complex eigenvalue as determined by the mean-field approximation for the case $a=b$. The vertical dotted line at $c^*=0.1143$ indicates the transition from oscillatory to ordinary behavior.

$$\langle \xi_i(t)\xi_j(t')\rangle = D_{ij}(x,y,v)\,\delta(t-t'). \tag{54}$$

The set of Langevin equations (51)–(53) describes noise oscillations similar to those shown in Fig. 2 but the transition to nonoscillatory behavior is of a distinct and more interesting kind.

Without noise, the densities x, y, and v approach their asymptotic values x^*, y^*, and v^* given by $f_1(x^*,y^*,v^*)=0$, $f_2(x^*,y^*,v^*)=0$, and $f_3(x^*,y^*,v^*)=0$. The stability of these solutions can be inferred from the eigenvalues of the Jacobian matrix J associated to the deterministic part of the Langevin equations calculated at the fixed point (x^*,y^*,v^*). For $a=b$ the eigenvalues of the Jacobian are shown in Fig. 4 as a function of c. For values of c smaller than $c_c=0.2$, the system shows an active stationary state. At the critical value $c=c_c$, determined by the vanishing of the dominant eigenvalue, there is a phase transition to the absorbing state. In the interval $c_0<c<c_c$, where $c_0=0.1675$, the three eigenvalues of the Jacobian matrix are real. In the interval $0<c<c_0$, however, two eigenvalues become complex and the other remains real. At $c=c^*$, where $c^*=0.1143$, the dominant real eigenvalue equals the dominant complex eigenvalue, that is $\gamma=\alpha$.

Inside the active state where the species coexist the system displays noise oscillations of the type phase-forgetting quasicycles in the interval $0<c<c^*$ and nonoscillatory behavior in the interval $c^*<c<c_c$. At $c=c^*$ there is thus a transition from the oscillatory to nonoscillatory behavior. The imaginary part of the complex eigenvalue, which is identified as the frequency of oscillations, may act as the order parameter characterizing the oscillatory state. In this case it jumps from a nonzero to a zero value. This discontinuous behavior is in better accordance with numerical simulations than the continuous behavior obtained from the first-order approximation. Indeed, a discontinuous behavior in the frequency of oscillations has been found for the present stochastic lattice-gas model by numerical simulations [44].

VII. DISCUSSIONS AND CONCLUSIONS

We have formulated a consistent and systematic procedure to derive Langevin equations describing undamped oscillations from stochastic lattice-gas models for predator-prey systems. The Langevin equations for the population densities are such that the noise decreases as one increases the size of the system. Without noise the oscillations are always damped. The noise plays then the crucial role of converting the damped into undamped oscillations. The undamped oscillations are characterized by time correlation functions whose asymptotic behavior is determined by the eigenvalues of the Jacobian associated to the deterministic part of the Langevin equations. The undamped oscillations of the type phase-forgetting quasicycles occur when the dominant eigenvalue possesses an imaginary part, identified with the frequency of the oscillations and regarded as the order parameter characterizing the oscillatory state.

According to the conceptual framework assumed here, phase-forgetting quasicycles or local oscillations in densities will emerge when the deterministic part of the Langevin equations presents a stable fixed point that is a focus. If the deterministic part predicted a limit cycle in the place of a stable focus fixed point this would result in the phase-remembering quasicycles or global oscillations in densities, which would then be observed even in the absence of noise. However, this situation did not happen in any of the two approximations used here.

We remark finally that the dominant eigenvalue of the Jacobian related to the deterministic part of the Langevin equations is to be identified as the dominant eigenvalue of the evolution operator associated to the master equation of the original stochastic lattice-gas model. More properly with the subdominant eigenvalue (or the eigenvalue "gap") because the dominant eigenvalue of an evolution operator is identically zero. The undamped time oscillations in the original stochastic lattice-gas model emerge then if the eigenvalue gap is complex, which is possible in irreversible but not in reversible stochastic dynamics.

APPENDIX

The master Eq. (2) can be written in the following equivalent form:

$$\frac{d}{dt}\langle F(\eta)\rangle = \sum_i \langle\{F(\eta^i) - F(\eta)\}w_i(\eta)\rangle, \tag{A1}$$

where $F(\eta)$ is any state function and the averages are determined using the probability distribution $P(\eta,t)$. Let us apply this formula to a particular type of state function $F(\eta)$ that depends on η only through $n=\Sigma_i n_i$ and $m=\Sigma_i m_i$. With the help of the projection variables p_i, n_i, and m_i, Eq. (A1) can be written as

$$\begin{aligned}\frac{d}{dt}\langle F(n,m)\rangle = {} & \sum_i \langle\{F(n+1,m) - F(n,m)\}p_i w_i(\eta)\rangle \\ & + \sum_i \langle\{F(n-1,m+1) - F(n,m)\}n_i w_i(\eta)\rangle \\ & + \sum_i \langle\{F(n,m-1) - F(n,m)\}m_i w_i(\eta)\rangle.\end{aligned} \tag{A2}$$

Next we use an approximation that replaces the summations

$$\sum_i p_i w_i(\eta), \quad \sum_i n_i w_i(\eta), \quad \sum_i m_i w_i(\eta), \tag{A3}$$

by quantities that depend on η only through $n=\Sigma_i n_i$ and $m=\Sigma_i m_i$. Notice that the last quantity is already of this form because it equals $c\Sigma_i m_i = cm$. Denoting these quantities respectively by

$$NA_{+0}(n,m), \quad NA_{-+}(n,m), \quad NA_{0-}(n,m), \tag{A4}$$

we get results (4)–(6) and Eq. (A2) can be written as

$$\frac{d}{dt}\langle F(n,m)\rangle = N\sum_{\sigma,\tau}\langle\{F(n+\sigma,m+\tau)-F(n,m)\}A_{\sigma\tau}(n,m)\rangle. \tag{A5}$$

Since now all quantities inside the brackets depend only on n and m we may interpret the averages as averages that are determined by means of the probability distribution $P(n,m,t)$ and Eq. (A5) becomes equivalent to the master Eq. (3). The same type of reasoning can be used to reach the master equation related to the approximation of the second order.

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