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Role of sub- and super-Poisson noise sources in population dynamics

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Abstract. In this paper we present a study on pulse noise sources characterized by sub- and super-Poisson statistics. We make a comparison with their uncorrelated counterpart. i.e. pulse noise with Poisson statistics, while showing that the correlation properties of sub- and super-Poisson noise sources can be efficiently applied to population dynamics. Specifically, we consider a termite population, described by a Langevin equation in the presence of a pulse noise source, and we study its dynamics and stability properties for two models. The first one describes a population of several colonies in a new territory with adverse environmental conditions. The second one considers the development of a single colony under the influence of attacks by predators.

Keywords: population dynamics, stochastic processes, fluctuation phenomena, correlation functions

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Contents

1. Introduction

During the last decades the effects of random fluctuations on the dynamics of natural systems has been widely and deeply investigated [1–5]. The random behaviour of biological systems and the role played by noise include bioinformatics [6, 7], population dynamics [8–11], infective desease and epidemics [12–14]. The presence of stochastic processes, which affect the dynamics of natural ecosystems [1, 2, 13, 15], the bacterial growth in food products [16], the inception and development of diseases due to genetic mutations [17–19], have been taken into account. It is worth noting that in population dynamics experimental data can be correctly reproduced by modeling the random fluctuations through multiplicative noise sources [20–34]. A pulse noise source, usually obtained as a Poisson white noise, has been already used to study thermal ratchets [36], noise-induced phase transitions [37], and population dynamics [38, 39]. In this paper we deepen this aspect, presenting a study, in the context of population dynamics, on the role played by the correlated pulse noise in the stability of a system. More in detail, we consider sub- and super-Poisson pulse noise sources and analyze their effects on the dynamics of a termite population [40–48].

When approaching population dynamics of termites, one has to consider that their modeling is more complicated than that of other animals, since they live in colonies (superorganisms). Appearance and growth of new colonies (termitary) can be considered as a jump up in number of individuals, since a new colony grows rapidly [49, 50].

These jumps or pulses in the population size are random with some kind of correlation. Therefore, the increase in population size is a random discrete jump process. These processes are usually modeled in the population dynamics as a random pulse process with short time correlations [15, 51]. Statistics of this pulse sequence defines population dynamics. Meanwhile, the decrease in population size is determined by the death of

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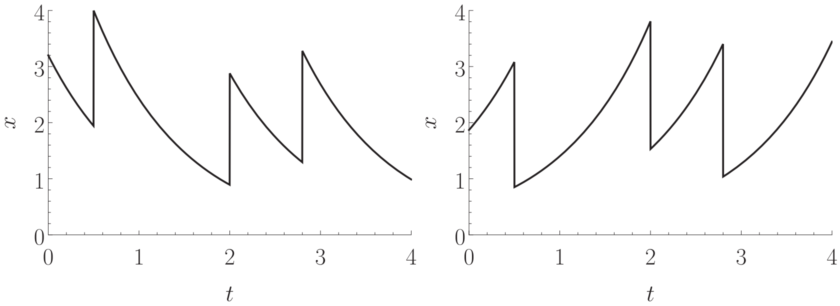
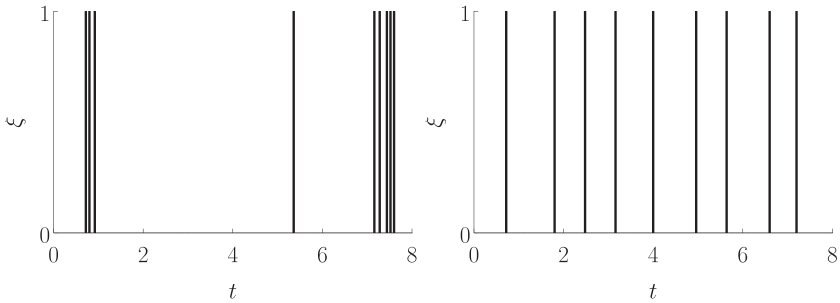


(a) pulse-like increase and slow decrease (b) pulse-like decrease and slow increase

Figure 1. Sample realization of population dynamics.



(a) super-Poisson (b) sub-Poisson

Figure 2. Renewal pulse process.

individuals and can be described as a continuous deterministic process [see figure 1(a)]. The correlated process which describes the starting of a new colony is a renewal process. This kind of process is described by a sequence or recurrent events, whose effect is to reset to zero the system's memory [52–58]. As a consequence, the interpulse distances or waiting times (WT's) are mutually independent random variables and the waiting time probability density function is the only basic property needed to define the process. The positive correlation between the pulses means that the presence of a pulse at a certain time instant increases the probability that another pulse appears during the immediately successive time interval. In this case, the pulse sequence includes subsequent pulses close to each other and far from each other. The variance of WT's is larger than for a Poisson process with the same average WT. This corresponds to super-Poisson statistics [see figure 2(a)]. Conversely, a sub-Poisson distribution is characterized by a smaller variance and a negative correlation [see figure 2(b)], for example, the dead-time Poisson noise [35].

In this paper a termite population in a new territory with adverse environmental conditions is studied from the point of view of the stability. Specifically, in order to determine the conditions under which the population tends to increase (instability) over the time or to decrease (stability) we use stochastic differential equation [4, 16, 59–61].

We also consider the case of only one large termite colony in the presence of favourable environmental conditions, i.e., sufficient food resources and optimal climatic

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situation, but subject to adverse biological conditions, i.e., predators, such as anteater or an army of ants, which could attack the termite colony, reducing the number of its individuals. These attacks can be described as a stochastic process modeled by a sequence of random negative pulses, which could also represent human attempts to regulate the termite population.

Finally we note that, unlike our previous works [13, 35], here the population shows over time a slow deterministic growth and a random pulse-down-decrease [see figure 1(b)].

The paper is organized as follows. In section 2, the renewal pulse process with sub- and super-Poisson statistics is described. In section 3, the stochastic deferential equation for the termite population is written and studied analytically. Results of numerical simulations are presented and discussed in section 4. Section 5 is devoted to concluding remarks.

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2. Renewal process

2.1. Process with Gamma distribution for inter-pulse intervals

Let us consider the stochastic process

$$\xi(t) = \sum_j f_0\, \delta(t - t_j), \tag{1}$$

consisting of δ-shape pulses with constant amplitude f_0, which, without any loss of generality, is convenient for both analytical and numerical study. Here t_j, which is a random variable, represents the time of the pulse appearance. The distances, or WT's, between two neighboring pulses, $\vartheta_j = t_j - t_{j-1}$, are independent identically distributed random variables. The mean of WT's, $\langle\vartheta\rangle = T$, is the conditional period of the process.

In the following, we use Gamma distribution for inter-pulse intervals ϑ with n as shape parameter, α as scale parameter, $\langle\vartheta\rangle = T = \alpha n$, and $\sigma_\vartheta^2 = \alpha^2 n$. If $n > 1$, equation (1) provides a process with sub-Poisson statistics. On the other side, $n < 1$ corresponds to a process governed by a super-Poisson statistics.

The spectral density of the process $\eta(t) = \xi(t) - \langle\xi\rangle$ is

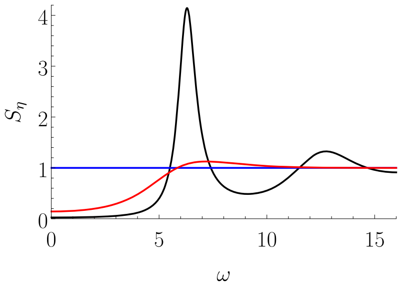
$$S_\eta(\omega) = \frac{f_0^2}{T}\frac{(1+\alpha^2\omega^2)^n - 1}{(1+\alpha^2\omega^2)^n + 1 - 2(1+\alpha^2\omega^2)^{n/2}\ \cos(n\ \arccos((1+\alpha^2\omega^2)^{-1/2}))}. \tag{2}$$

In view of using this kind of processes in a stochastic differential equation and modeling some population dynamics, e.g., time evolution of termite colonies, the following expression is obtained:

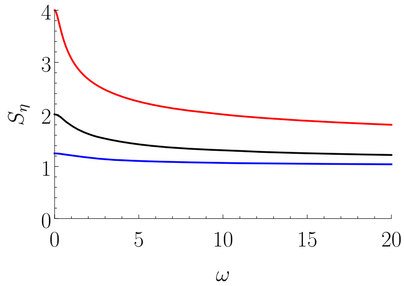
$$S_\eta(0) = \frac{f_0^2}{Tn}. \tag{3}$$

For the case of Poisson statistics ($n = 1$) we get a constant solution.

The spectral densities and their properties are illustrated in figure 3(a) for $n \geqslant 1$. The larger n the more periodical the process is. The super-Poisson case is presented in figure 3(b) for $n < 1$. Note that the main part of the plot is approximately horizontal.



(a) sub-Poisson and Poisson processes: $n = 40$ (black), $n = 7$ (red), $n = 1$ (blue).



(b) super-Poisson process: $n = 0.25$ (red), $n = 0.5$ (black), $n = 0.8$ (blue).

Figure 3. Spectral density of the sub- and super-Poisson processes for different values of the shape parameter ($T = 1,\ f_0 = 1$).

2.2. Strongly super-Poisson process replaced by the corresponding Poisson one

In the case of a strongly super-Poisson process the pulses arrive as clusters, that is as packages consisting of several pulses close to each other. These clusters can be easily distinguished since the distances between them are quite large in comparison with their size. In figure 2(a) two such clusters are presented with three and five pulses. Therefore, we can replace the super-Poisson process of single pulses with the corresponding Poisson sequence of large pulses-clusters, for which the spectral density is constant. That corresponds well to the horizontal plot in figure 3(b). Let N be the average number of pulses in a cluster. In this case, the amplitude of this large pulses-cluster is $f_{\mathrm{P}} = Nf_0$ and the average distance between the clusters is $T_{\mathrm{P}} = NT$. The main characteristic of a pulse process is the variance of the WT's. For this process, characterized by the presence of pulse-clusters, $\sigma_{\mathrm{P}}^2 = T_{\mathrm{P}}^2 = N^2T$, since the WT's are distributed exponentially. This variance is equal to the variance of the initial super-Poisson process $\sigma_\vartheta^2 = T^2/n$. As a result, $N = n^{-1/2}$. The spectral density for the Poisson process in accordance with equation (2) is

$$S_{\mathrm{P}}(\omega) = \frac{f_{\mathrm{P}}^2}{T_{\mathrm{P}}} = \frac{f_0^2}{T\sqrt{n}}. \tag{4}$$

This spectral density at $\omega = 0$ is less than $S_\eta(0)$ in equation (3).

3. Stability of the population under the influence of non-Poisson noise

The simplest equation to describe a stable-unstable system reads

$$\dot{x} = -ax + x\xi(t), \tag{5}$$

where $x(t)$ is the number of species and $\xi(t)$ is the pulse process (1) characterised by the noise intensity (3).

In the case of $a > 0$ and $f_0 > 0$ [see figure 1(a)], this equation describes two processes: (i) deterministic exponential decrease in population, consisting of many colonies, with the rate a describing the entire population dynamics except the appearance of new colonies; (ii) the building up process and development of new termitaries, which is presented as the pulse process $\xi(t)$ given by equation (1).

In the case of $a < 0$ and $f_0 < 0$ [see figure 1(b)], this equation describes development of a single colony under the influence of attacks by predators or humans. The rate a represents an increase in the colony size. At the beginning of a new colony development, the population increases exponentially [63]. The queen physogastry develops by a positive feed-back mechanism: as more ovarioles become functional, more eggs are laid, more workers emerge, more forage is collected for the colony, and more food is brought to the queen [41]. This model with pulse-like decrease of single colony does not contradict to the previous model for a large number of colonies, since these attacks are uncorrelated and their results are small in comparison with the large many-colonies population.

Under conditions $|f_0| \ll x$ and $T \ll |a|^{-1}$, the analytical solution to equation (5) is obtained

$$\langle x\left(t\right)\rangle = x_0\ \mathrm{e}^{-at}\left\langle \exp\left\{\int_0^t \xi\left(\tau\right)\mathrm{d}\tau\right\}\right\rangle. \tag{6}$$

Now we define a new random variable, $W(t)= \int_0^t \xi(\tau)\mathrm{d}\tau$. According to the central limit theorem, this variable has a Gaussian distribution. Its statistical properties therefore can be fully described by the first moment, defined by the average number of pulses for large enough t, and the variance which read, respectively,

$$\langle W(t)\rangle = \left\langle \int_0^t \xi(\tau)\mathrm{d}\tau\right\rangle = f_0\langle m\rangle = \frac{f_0}{T}\,t \tag{7}$$

and

$$\sigma_W^2(t) = \left\langle \int_0^t \left(\xi(\tau') - \frac{f_0}{T}\right)\mathrm{d}\tau' \int_0^t \left(\xi(\tau'') - \frac{f_0}{T}\right)\mathrm{d}\tau''\right\rangle. \tag{8}$$

Using the definition of correlation function $K_\eta(\tau'' - \tau')$ after a change of variables we obtain

$$\sigma_W^2(t) = 2\int_0^t (t-\tau)K_\eta(\tau)\mathrm{d}\tau. \tag{9}$$

Here we are interested in the final outcome of the population development, which depends on the stability/instability condition of the system. In our analysis we therefore consider a time t large respect to the correlation time. Under this condition, we get

$$\sigma_W^2(t) \approx t\int_{-\infty}^{\infty} K_\eta(\tau)\mathrm{d}\tau = S_\eta(0)t = \frac{f_0^2\sigma_\vartheta^2}{T^3}\,t = f_0^2\sigma_m^2. \tag{10}$$

Using the definition of characteristic function $C(\omega)$ of the Gaussian distribution, from equation (6) we obtain

$$\langle x(t)\rangle = x_0\ \mathrm{e}^{-at}C(-i) = x_0\ \exp\left\{\left(\frac{f_0}{T} + \frac{f_0^2\sigma_\vartheta^2}{2T^3} - a\right)t\right\}. \tag{11}$$

Equation (11) indicates that the system is stable for $a > a_{\mathrm{cr}}$, where

$$a_{\mathrm{cr}} = \frac{f_0}{T} + \frac{f_0^2 \sigma_\vartheta^2}{2T^3} = \frac{f_0}{T} + \frac{f_0^2}{2Tn} \tag{12}$$

is the critical value of the relaxation parameter.

4. Results and discussion

In this section, we present the results obtained by solving numerically equation (5) and compare them with the analytical findings obtained in section 3 for the sub- and super-Poisson random process. To generate a delayed pulse train with a Gamma distribution we use the Marsaglia and Tsang method [65]. As a pseudorandom number generator we exploit the Mersenne twister method [66]. The averaging is performed over 10^7 stochastic realizations in each analysed case. In all subsequent calculations the mean pulse distance is $T = 1$ and the initial condition is set at $x_0 = 1$. The simulation time is $T_{\max} = 4 \times 10^5$.

For the parameter a we introduce a critical value, a_{cr}, defined as the value of a for which the stability-instability transition is observed. Then we investigate the behaviour of the critical value of the relaxation parameter a_{cr} as a function of the parameters of the system. Figure 4 shows the dependence of a_{cr} ($a > 0$) on n for the process with a pulse-shaped increase and a slow decrease [see figure 1(a)]. The analytical results obtained from equation (12) are represented by solid lines, those obtained from numerical approach are shown as black squares for $f_0 = 0.0101$ and red circles for $f_0 = 0.01$. A good agreement with the sub-Poisson processes ($n > 1$) is observed. On the other side, for noise sources with a strongly super-Poisson statistics ($n < 1$) a noticeable disagreement appears. This can be explained noting that in this case the conditions used to get the analytical solution [see equation (6)] are not satisfied. The pulses indeed arrive together, forming clusters with several pulses very close to each other (see subsection 2.2). As a result, the dynamics of $x(t)$ is far from being continuous. Dashed lines represent approximated results obtained by using the corresponding Poisson processes in accordance with equations (4) in (10) and (12). We note that, for a super-Poisson process with $n \ll 1$, the pulse-cluster approximation matches numerical results better than the single-pulse model.

As a conclusion, the main result is that the population is more stable in the case of sub-Poisson noise than for super-Poisson. In other words, positive correlations ($S(0) > 1$) in new colonies appearances lead to faster increase in the population size than negative ones ($S(0) > 1$), if all other parameters are fixed. Positive correlations describe, for example, a situation in which a new colony produces new couples and, as a consequence, the initiation of new colonies. The first colony can also attract symbionts that contribute to the development and survival of the successive colony. The first colony can also contribute more directly, for example, by digging in the wood tunnels which improve the possibility of development of a second colony. As a consequence of such mechanisms of positive correlations, population density increases exponentially. On the other hand, negative correlation (sub-Poisson statistics) can play a crucial role. A competition evidently causes an anticorrelation between the new colonies. Competition between two colonies always comes into play as an agonistic behaviour, resulting in a

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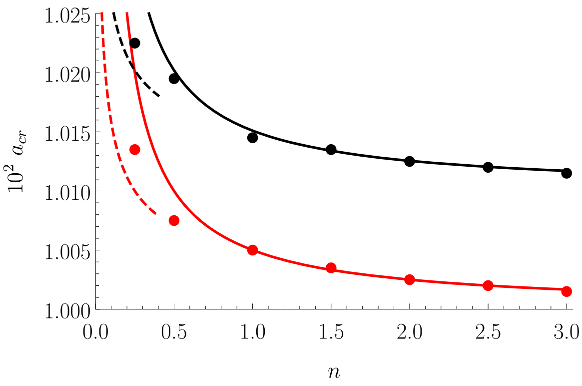

Figure 4. Plot of the critical relaxation parameter a_{cr} vs the shape parameter n for the process with a pulse-shaped increase and a slow decrease for different values of pulse amplitude, namely $f_0 = 0.0101$ (black), $f_0 = 0.01$ (red). Analytical [solid lines from equation (12), dashed lines from equation (4)] and numerical (dots) results are compared.

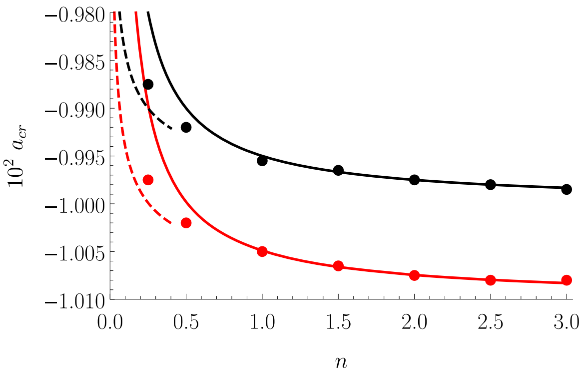

Figure 5. Plot of the critical relaxation parameter a_{cr} vs the shape parameter n for the process with a pulse-shaped decrease and a slow increase for different values of pulse amplitude, namely $f_0 = -0.0101$ (black), $f_0 = -0.01$ (red). Analytical [solid lines from equation (12), dashed lines from equation (4)] and numerical (dots) results are compared.

fight between the two colonies. This fight can cause mortality on both sides and, in some cases, the gain or loss of territory [62]. As a result, the appearance of a colony contributes negatively to the appearance of another colony in a very short time, making its 'emergence' less likely respect to the uncorrelated case (Poisson statistics). This mechanism introduces a certain periodicity in the population dynamics and prevents exponential growth.

Figure 5 shows the behaviour of a_{cr} $(a < 0)$ as a function of n for the process with a pulse-shaped decrease and a slow increase [see figure 1(b)]. The analytical results obtained from equation (12) are represented by solid lines, those obtained from numerical simulations are shown as black squares for $f_0 = -0.0101$ and red circles for $f_0 = -0.01$.

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As in figure 4, dashed lines represent approximated results obtained by the corresponding Poisson processes in accordance with equation (4). Also in this case we note that, for a super-Poisson process with $n \ll 1$, the pulse-cluster approximation matches numerical results better than the single-pulse model.

This analysis allows to conclude that, for fixed values of the parameter a, the noise amplitude f_0 and the noise period T, larger values of the parameter n (sub-Poisson statistics) produce a greater stability of the system.

We note that the attacks can be negatively correlated in the following way: after exhausting a colony in a given area, predator may be obliged to move to other areas, allowing the previously attacked colony to recover [64]. Such periodical attacks maintain the population density stable or even constant.

On the contrary, positive correlation can correspond to multiple attacks by the same predator and, in particular, to the fact that the first attack destroys the termitary while reducing the possibility of defense, with a consequent increase in the probability of undergoing other attacks also by different predators. In comparison with the case of periodical attacks characterized by the same values of the other parameters, including the average WT, T, these positively correlated negative pulses lead to an exponential increase in population size. The constant T corresponds to long WT's after several successive attacks. During these long time, the population increases exponentially. This can give practical advice for human efforts to reduce the termite population. These works are more effective if they are performed regularly.

We wish also note that the choice of termites for this study is based on the following motivations: (i) termite colonies consist of numerous individuals, which allows to get results statistically significative; (ii) they can be counted by colonies, therefore a clear relationship between the termitary size and the number of individuals exists. For example, a correlation was established between the nest volume and the logarithm of the total population [63].

Moreover, the model analyzed in this work combines a continuous description for the size of each colony, represented through its population concentration, with a discrete description for the number of colonies. Finally we notice that this model can also be applied to different context of population dynamics, such as the growth of a virus population, which is typically counted in terms of number of colonies, with each colony corresponding to an infected person. Epidemiological equations, which are usually written for the number of infected people [15], could be modified by taking into account the number of virus units, i.e., the viral load, for each infected person. Suitable modifications of equation (5) could therefore allow to develop more realistic epidemiological models.

5. Conclusions

In this paper we studied the stability conditions for the dynamics of a termite population. The effect of these correlations can be estimated by using a stochastic differential equation with a noise source modeled as a renewal process with a suitable statistics. Starting from a previous study [35], where the stability of such a system was investigated in the presence of a multiplicative positive-defined sub-Poisson pulse process, we extended here the analysis to the case of a super-Poisson noise source and negative-defined pulse processes. Specifically, we analyzed the dynamics of the termite population in the presence of a noise source with different statistical properties, ranging from sub- to super-Poisson processes, in two different cases: (i) positive-defined pulses; (ii) negative-defined pulses. From a mathematical point of view the statistics of the WT's is described by Gamma distribution, with n being the shape parameter, responsible for the specific statistics. As one can argue, the stability of the termite population depends on the statistics of the pulse process which describes the sharp changes in the population density. In particular, we observed that, as n decreases, which corresponds to positive correlations among pulses, the system becomes less stable.

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