Fluctuations in the Lotka-Volterra Model

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(Received April 10, 1981)

Oscillations and Fluctuations in the Lotka-Volterra model are investigated by the method of system size expansion.

Fluctuations around the most probable path show an anomolous behavior: Time-evolution of envelope functions of the fluctuations becomes very fast indicating rapid diffusion in populations of the species.

§ 1. Introduction.

An interesting mathematical model describing competing biological species was introduced by Lotka and Volterra and has been studied by many authors.[1] Most of the theoretical work, however, is confined to behaviors of deterministic motion (the most probable path). We examine in this note fluctuation phenomena around the most probable path with the aid of the method of system size expansion.[2,3] We employ the simplified form of the method[4,5] used in the quantum mechanical theory of nonequilibrium systems (superradiance[4] and a dissipative spin system[5]).

§ 2. Deterministic Motion.

The Lotka-Volterra model is represented by coupled equations:[1]

$$\frac{dN_1}{dt}=(\varepsilon_1-\gamma_1 N_2)N_1 \tag{1a}$$

and

$$\frac{dN_2}{dt}=(-\varepsilon_2+\gamma_2 N_1)N_2\,. \tag{1b}$$

We illustrate the biological content of (1) as follows: These equations describe situations in which the species 2 eat the species 1: This is reflected in the nonlinear ("collision") terms in (1). We assume that all the species are composed of "adults" and the preys have sufficient foods. When there is no interaction between these species, the population of the prey (species 1) N_1 will increase because the preys have the sufficient foods; the growing rate is assumed to be ε_1 ($\varepsilon_1>0$). While, if the preys are absent, the population of the predator N_2 will decrease because the predator has no food; the decreasing rate is ε_2

($\varepsilon_2>0$). When we introduce interactions between the species, the population of the preys N_1 will decrease as that of the predators increase. In the first approxination, the growing rate is considered to be $\varepsilon_1-\gamma_1 N_2$ ($\gamma_1>0$). Conversely the population of the predators will increase when that of the preys increase; the growing rate is $-\varepsilon_2+\gamma_2 N_2$ ($\gamma_2>0$). Consequently we have the coupled equations (1).

In the following we discuss the case of $\gamma_1=\gamma_2$. We rewrite (1) in the form:

$$\begin{aligned} \frac{dX_1}{dt}&=K_1X_1-\varepsilon K_2X_1X_2 \\ \frac{dX_2}{dt}&=\varepsilon K_2X_1X_2-K_3X_2\,. \end{aligned} \tag{1$'$}$$

In (1)$'$ the variables X_1 and X_2 are considered to be "macroscopic". Namely we have

$$X_1,\ X_2=O(\Omega)$$

where $\Omega\equiv\varepsilon^{-1}$ specifies size of the system.

§ 3. Master Equation.

Following the method due to Nicolis[6] we derive the master equation consistent with the Volterra model. First we regard (1)$'$ as conservation-of-mass equations of the following set of irreversible autocatalytic chemical reactions:

$$A+X_1 \xrightarrow{k_1} 2X_1 \tag{2a}$$

$$X_1+X_2 \xrightarrow{k_2} 2X_2 \tag{2b}$$

$$X_2+D \xrightarrow{k_3} E+D \tag{2c}$$

with

$$k_1A=K_1$$

$$k_3D=K_3$$

$$k_2=\varepsilon K_2$$

where k_1, k_2 and k_3 are the constants of velocity in the chemical reaction: (2a) represents a situation in which X_1 grows up to eat A, whereas (2b) shows that X_2 grows up to eat X_1, and in (2c) X_2 dies out to interact with D and yield an increase of E. Thus (2) is fully consistent with (1)$'$.

From a set of equations, (2), we can construct a master equation:

$$\begin{aligned} \frac{\partial}{\partial t}P(X_1, X_2, t)&=K_1(X_1-1)P(X_1-1, X_2, t)-K_1X_1P(X_1, X_2, t) \\ &+K_2\varepsilon(X_1+1)(X_2-1)P(X_1+1, X_2-1, t)-K_2\varepsilon X_1X_2P(X_1, X_2, t) \\ &+K_3(X_2+1)P(X_1, X_2+1, t)-K_3X_2P(X_1, X_2, t)\,. \end{aligned}$$

Here we scale the variables X_1 and X_2 by Ω changing into "intensive variables":

$$X_1/\Omega = x_1$$

and

$$X_2/\Omega = x_2 .$$

By a requirement of normalization for the probability function, we have

$$P(x_1, x_2, t) = \Omega^2 P(X_1, X_2, t) .$$

Thus we have the following master equation for x_1 and x_2:

$$\begin{aligned}\varepsilon \frac{\partial}{\partial t} P(x_1, x_2, t) &= K_1 \left\{ \exp\left(-\varepsilon \frac{\partial}{\partial x_1}\right) - 1 \right\} x_1 P(x_1, x_2, t) \\ &+ K_2 \left\{ \exp\left(\varepsilon \frac{\partial}{\partial x_1}\right) \exp\left(-\varepsilon \frac{\partial}{\partial x_2}\right) - 1 \right\} x_1 x_2 P(x_1, x_2, t) \\ &+ K_3 \left\{ \exp\left(\varepsilon \frac{\partial}{\partial x_2}\right) - 1 \right\} x_2 P(x_1, x_2, t) .\end{aligned} \tag{3}$$

From (3) we can calculate the mean values and fluctuations of x_1 and x_2.

§4. Ω-expansion.

From (3) we find moment equations of x_1 and x_2:

$$\frac{\partial}{\partial t} \langle x_1 \rangle = K_1 \langle x_1 \rangle - K_2 \langle x_1 x_2 \rangle$$

$$\frac{\partial}{\partial t} \langle x_2 \rangle = K_2 \langle x_1 x_2 \rangle - K_3 \langle x_2 \rangle$$

$$\frac{\partial}{\partial t} \langle x_1^2 \rangle = 2K_1 \langle x_1^2 \rangle - 2K_2 \langle x_1^2 x_2 \rangle + K_1 \varepsilon \langle x_1 \rangle + K_3 \varepsilon \langle x_1 x_2 \rangle$$

$$\frac{\partial}{\partial t} \langle x_2^2 \rangle = 2K_2 \langle x_1 x_2^2 \rangle - 2K_3 \langle x_2^2 \rangle + K_2 \varepsilon \langle x_1 x_2 \rangle + K_3 \varepsilon \langle x_2 \rangle$$

$$\frac{\partial}{\partial t} \langle x_1 x_2 \rangle = (K_1 - K_3 - \varepsilon K_2) \langle x_1 x_2 \rangle - K_2 \langle x_1 x_2^2 \rangle + K_2 \langle x_1^2 x_2 \rangle .$$

We can further transform the above moment equations into cumulant equations using the relations like

$$\langle x_\mu \rangle = \langle x_\mu \rangle_c$$

and

$$\langle x_\mu x_\nu \rangle = \langle x_\mu x_\nu \rangle_c + \langle x_\mu \rangle \langle x_\nu \rangle \qquad (\mu, \nu = 1 \text{ and } 2) .$$

Using the method of system size expansion[2-5], we have the following properties of the cumulants:

$$\langle x_\mu \rangle_c = y_\mu + \varepsilon u_\mu + O(\varepsilon^2) ,$$

$$\langle x_\mu x_\nu \rangle_c = \varepsilon \sigma_{\mu\nu} + O(\varepsilon^2)$$

and

$$\langle x_\mu x_\nu x_\lambda \rangle_c = O(\varepsilon^2) \qquad (\mu,\ \nu,\ \lambda=1 \text{ and } 2),$$

giving a set of equations:

$$\begin{aligned}
\dot{y}_1 &= K_1 y_1 - K_2 y_1 y_2 \\
\dot{y}_2 &= K_2 y_1 y_2 - K_3 y_2 \\
\dot{u}_1 &= K_1 u_1 - K_2(\sigma_{12} + u_1 y_2 + y_1 u_2) \\
\dot{u}_2 &= K_2(\sigma_{12} + y_1 u_2 + u_1 y_2) - K_3 u_2 \\
\dot{\sigma}_{11} &= (2K_1 - 2K_2 y_2)\sigma_{11} - 2K_2 y_1 \sigma_{12} + K_1 y_1 + K_2 y_1 y_2 \\
\dot{\sigma}_{22} &= 2K_2 y_2 \sigma_{12} + (2K_2 y_1 - 2K_3)\sigma_{22} + K_2 y_1 y_2 + K_3 y_2 \\
\dot{\sigma}_{12} &= K_2 y_2 \sigma_{11} + (K_1 - K_3 - K_2 y_2 + K_2 y_1)\sigma_{12} - K_2 y_1 \sigma_{22} - K_2 y_1 y_2 .
\end{aligned} \tag{4}$$

We solved (4) numerically with the initial conditions given by

$$\begin{aligned}
&y_1(0)=0.5, \qquad y_2(0)=2.0, \\
&u_1(0)=u_2(0)=1.0, \\
&\sigma_{11}(0)=\sigma_{22}(0)=\sigma_{12}(0)=0.0,
\end{aligned}$$

and

$$K_1=K_2=K_3=1.0.$$

The results are shown in Figs. 1-6. We see the known (usual) oscillations[1] of y_1 and y_2 from Fig. 1. From other figures, however, we find the unusual be-

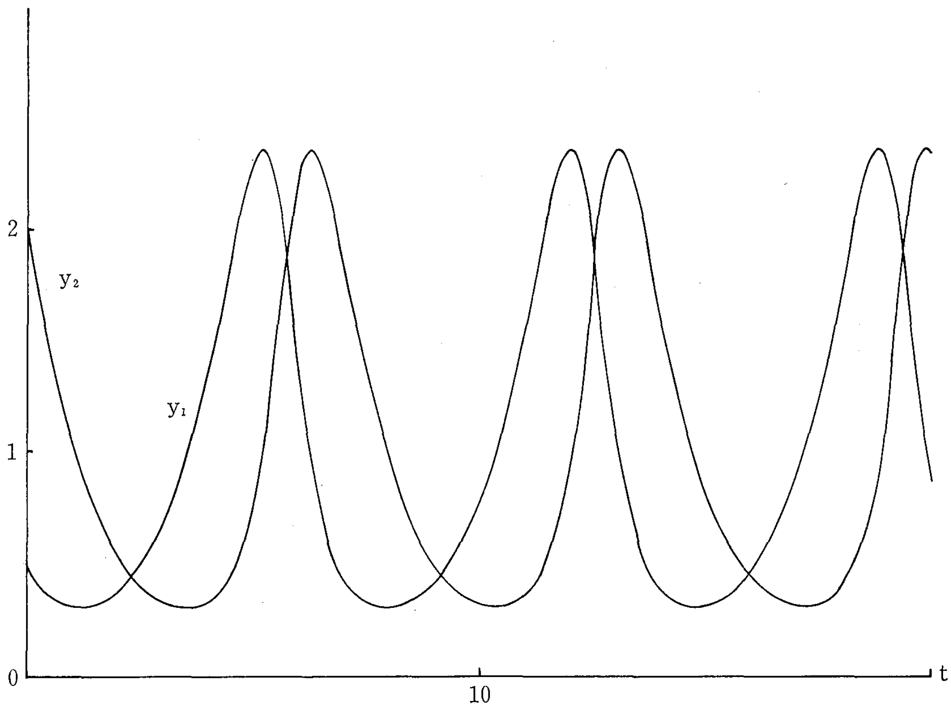

Fig. 1.

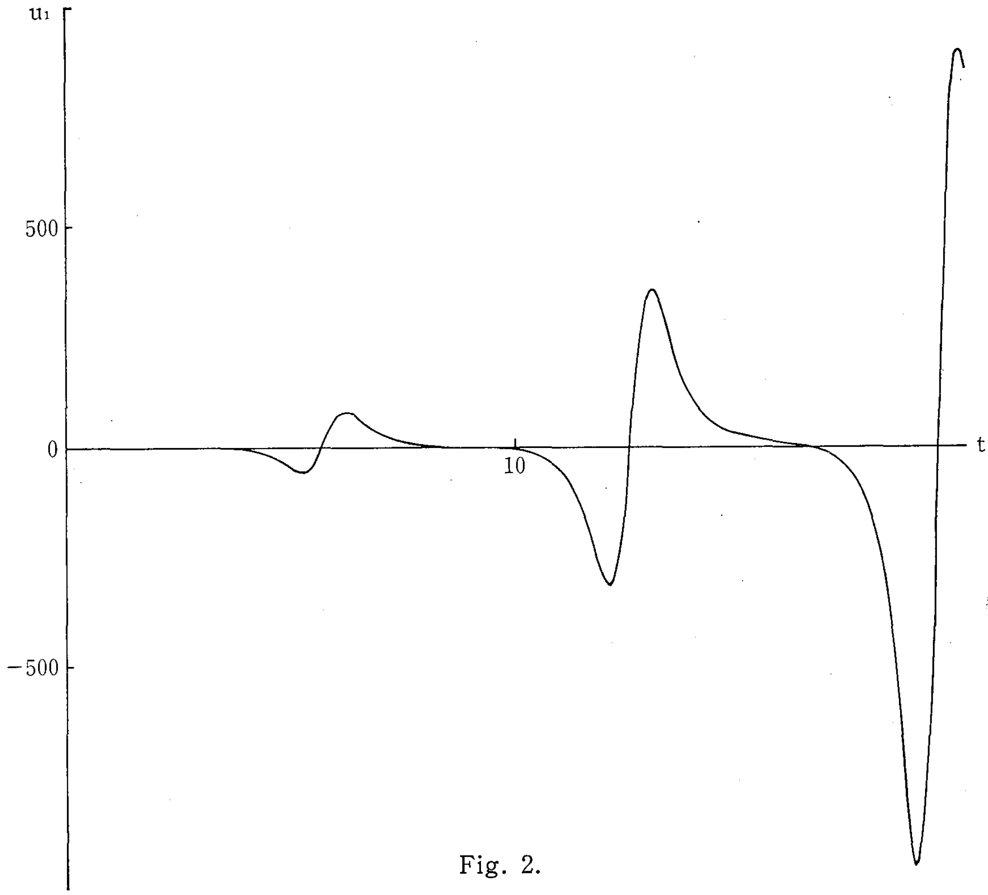

Fig. 2.

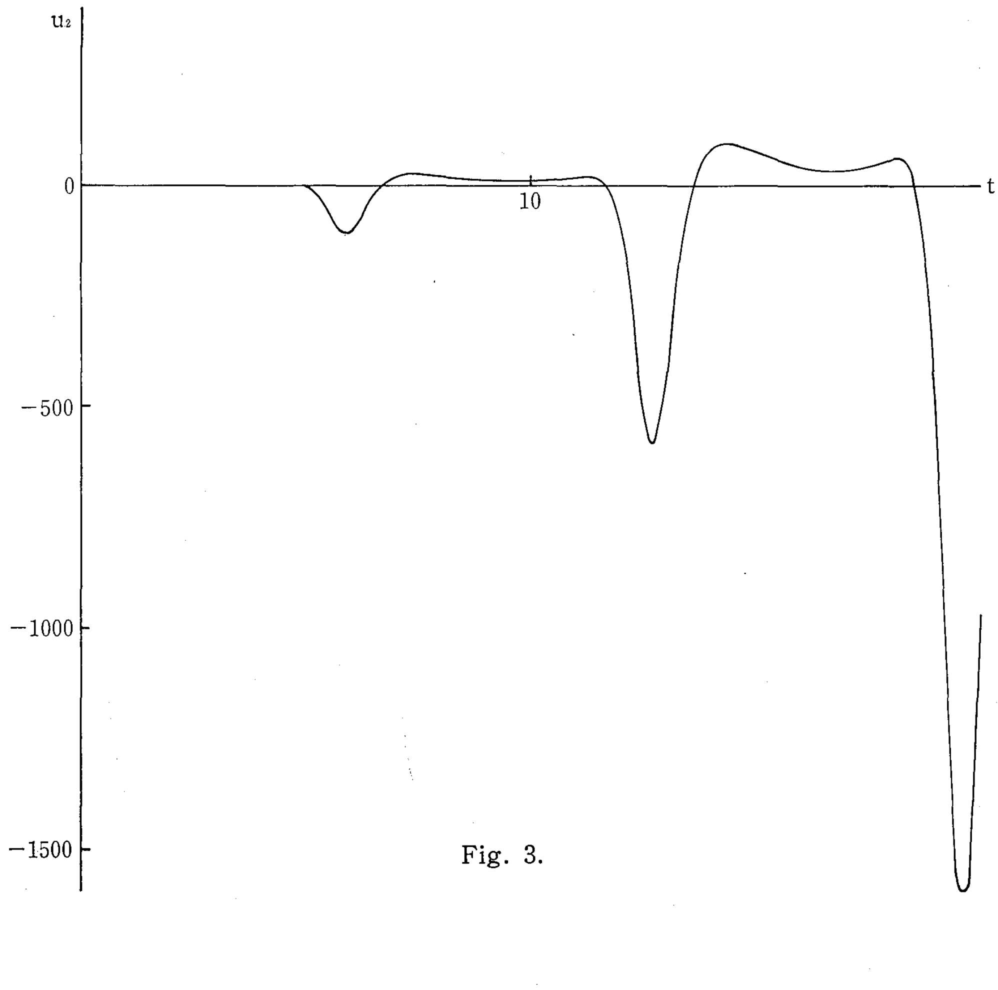

Fig. 3.

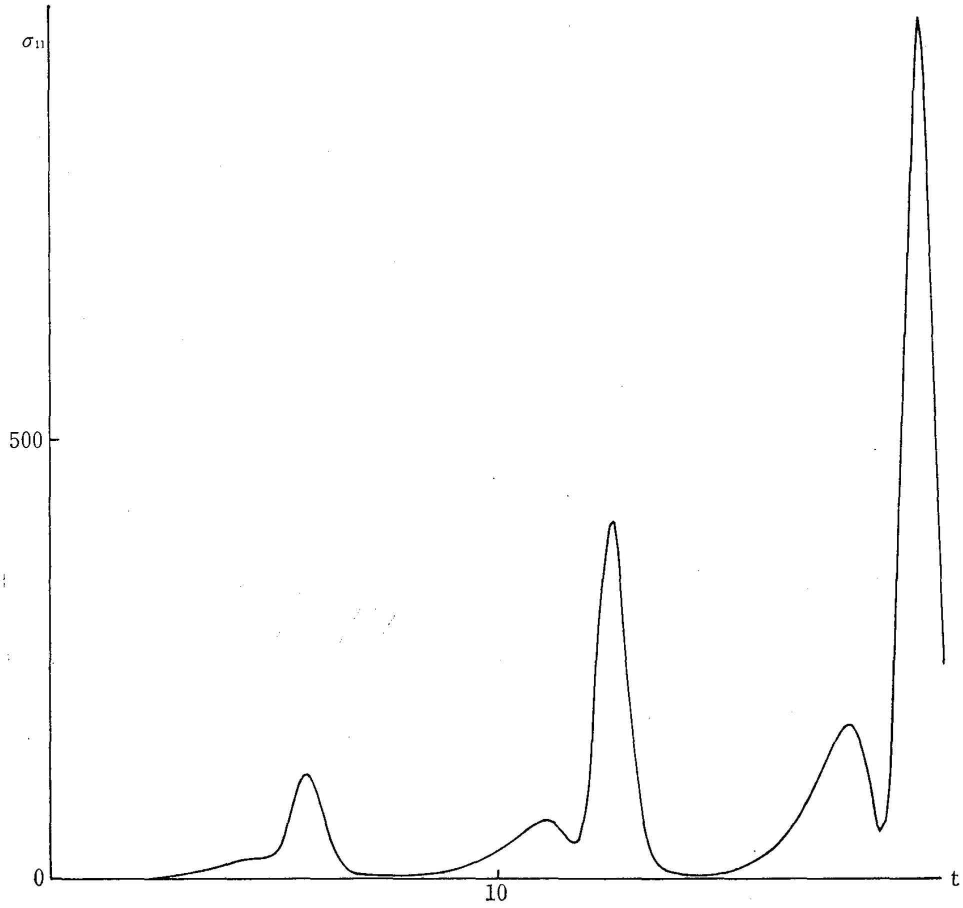

Fig. 4.

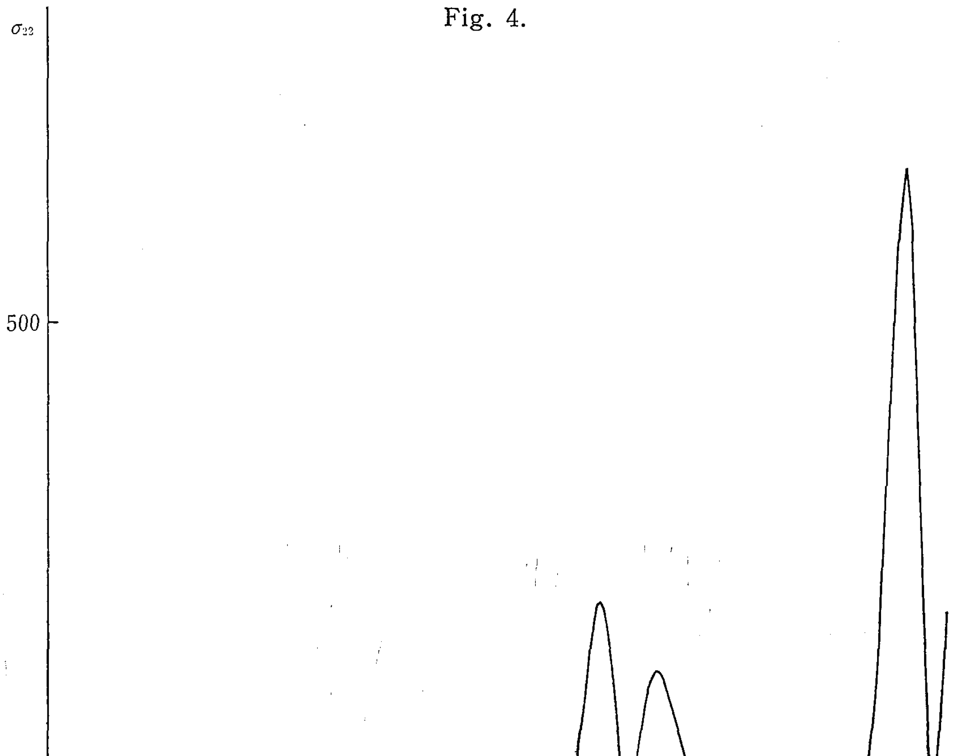

Fig. 5.

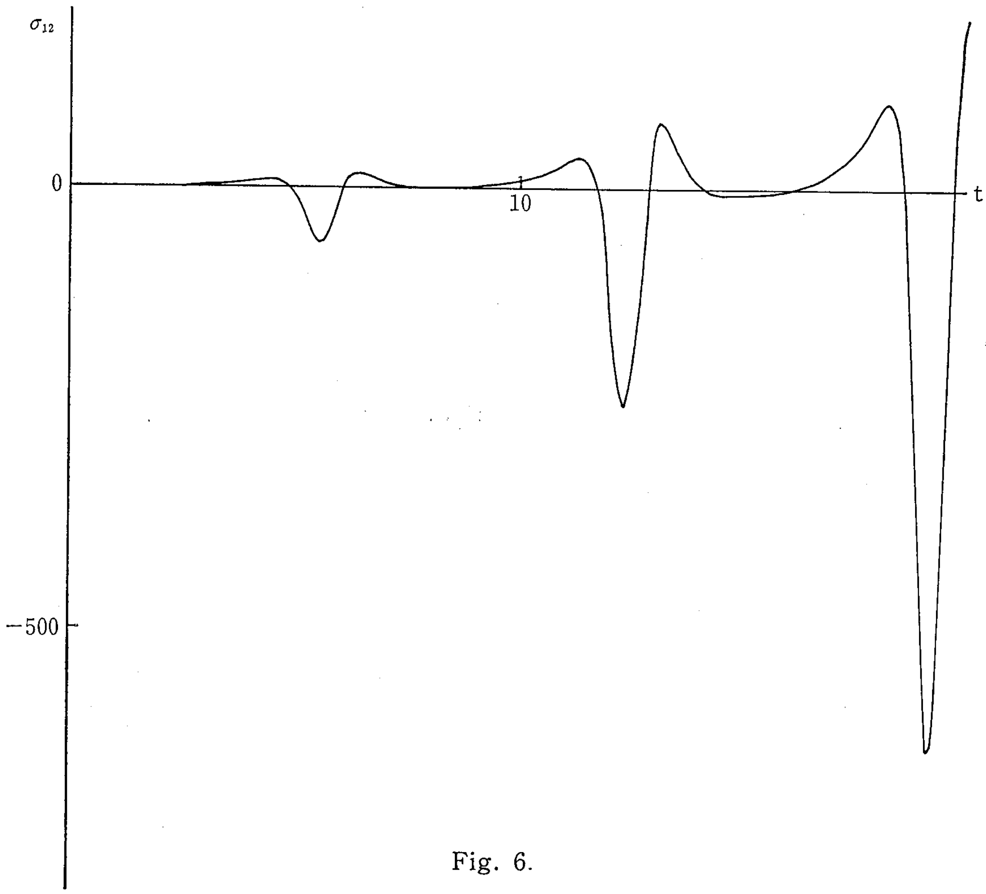

Fig. 6.

haviors of u's and σ's: the envelope of these quantities increases very rapidly as a function of time.

§ 5. Remarks.

The results of our numerical calculations show the anomalous behaviors of σ and u: These quantities grow very rapidly as the time evolves. This is considered to be a sort of diffusion phenomena. In the Brownian motion, for instance, we have

$$\sigma = 2Dt$$

where D is the diffusion constant. We have an analogous situation in ref. 5). In our case, however, the time-evolution of σ is faster than t^1 indicating very rapid diffusion-like phenomena of this system.

Thus the Lotka-Volterra model is seen to be quite "sensitive" to the fluctuations. The stable deterministic motion of the original model is completely destroyed by an introduction of the fluctuations. Therefore it may also be interesting to construct a model with a stable deterministic motion against the fluctuations.

Acknowledgement.

We are grateful to Professor N. Hashitsume for valuable discussions.

References

[1] See for a review; N.S. Goel, S.C. Maitra and E.W. Montroll: Rev. Mod. Phys. **43** (1971) 231.
[2] N.G. van Kampen: Can. J. Phys. **39** (1961) 551.
[3] R. Kuho, K. Matsuo and K. Kitahara: J. Stat. Phys. **9** (1973) 51.
[4] Y. Takahashi and F. Shibata: J. Stat. Phys. **14** (1976) 67.
[5] F. Shibata, S. Chaturvedi and Y. Saito: Z. Phys. B**36** (1979) 195.
[6] G. Nicolis: J. Stat. Phys. **6** (1972) 195.