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# ON THE GIBBS ENSEMBLE DESCRIPTION OF BIOLOGICAL SYSTEMS

by

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Summary.- The conditions under which the macroscopic models described by equations of the type $\dot{x} = \psi(x)$ may be treated by Gibbs ensemble theory are studied, following the scheme proposed by Kerner. The general theory is applied to several well-known models existing in the literature.

## I.- Introduction.-

There exist in nature ensembles (populations containing several interacting species, political parties, chemical components reacting in a coupled form, the nervous system,...) whose elements influence each other by means of competition and cooperation processes. Starting from fundamental principles or using intuitive ideas, we can construct theoretical models describing the properties of a certain number of those natural ensembles.

In the present paper we will consider macroscopic models whose equations of motion are of the type

$$\dot{x} = \psi(x)$$

where $x \equiv (x_1, x_2,..,x_i,...)$ and $\dot{x} \equiv dx/dt$. The role of this equation in our problem is analogous to the role of Hamilton's equations in Classical Mechanics.

The x's are macrocopic variables in the sense that they can be controlled in the experiments and, therefore, macroscopic information about them is available. If we want to introduce in our model a description of the fluctuations, we have two possibilities.- First, we can consider that the equations of motion are valid for certain stochastic variables by just adding a fluctuating term whose avarage value is zero (Langevin type description). Or, second, we can consider that the macroscopic variables (which define a macrostate of the system) correspond to average values of microscopic variables (which define a microstate of the system) and introduce an ensemble of microstates compatible with a given macrostate. This ensemble is characterized by the macroscopic information about the system and each microstate evolves in time according to the equations of motion for the model. This second method is the one that will be followed in this paper.

We are interested in the fluctuations appearing in a macroscopic system at equilibrium. We, thus, construct an appropiate ensemble to describe a stationary state. To parallel classical Statistical Mechanics with the introduction of an equal a priori probabilities postulate, we need to define a phase space, a Liouville theorem in this phase space ($\partial\dot{x}_i/\partial x_i = 0$) and a constant of motion playing the role of a Hamilton function.

We then, admit that the macroscopic values correspond to the average values over the ensemble of the microscopic variables.

This scheme was proposed by Kerner (1957) and applied to Volterra's ecological model (Volterra, 1931; Goel, Maitra and Montroll, 1971).

The purpose of this paper is to investigate what kind of models (biological, biochemical, sociological,...) allow a similar treatment, thus developping Kerner's theory in a more general form.

The paper is planned as follows. Kerner's work is briefly described for reference purpose in Section II. In Section III the general theory is developped and the conditions for the applicability of a statistical description are established. Finally, in Section IV the theory is applied to several models and some conclusions are presented.

## II. Statical Mechanical Formulation of Volterra's model.-

Volterra's ecological model for two interacting species is described by the equations

$$\dot{N}_1 = a_1N_1 - b_1N_1N_2 \qquad (1a)$$

$$\dot{N}_2 = -a_2N_2 + b_2N_1N_2 \qquad (1b)$$

where $N_1$ represents the number of individuals of the prey species and $N_2$ the number of predators. The constants $a_1$, $a_2$, $b_1$, $b_2$ are assumed to be positive.

Kerner (1957) showed the existence of a time independent function

$$G(N_1,N_2) = (b_2N_1 - a_2\log N_1) + (b_1N_2 - a_1\log N_2) \qquad (2)$$

This G is a constant of the motion described by Eq. (1). Furthermore, if we write the equations of motion in terms of a new set of variables $x_i = \log N_i$ we can prove a Liouville's theorem in the x-space )phase space).

Kerner's (1957, 1971) idea consists in associating with each equilibrium macroscopic state (macrostate), an ensemble of accesible microstates, all of them with the same probability (equal a priori probabilities principle). Each microstate corresponds to one of the possible sets of values $\{x_i\}$ compatible with the given value of G and is represented by a point in the phase space $\{x_1,...x_n\}$. The ensemble is thus represented by a cloud of points in phase space. The density of points in phase space $\rho(x_1,...,x_n)$ obeys a continuity equation, following from Liouville's theorem. If we now assume that time averages of a macroscopic system are identical with average values taken over the ensemble (ergodic hypothesis) we can construct a "Statistical Mechanics" of the system and obtain a "thermodynamical" description of it.

If the system is described by a microcanonical ensemble, the distribution function is $\rho = C\delta(G-G_0)$, where C is the normalization constant. If a canonical ensemble is used, then the distribution function is $\rho = Z^{-1}\exp(-G/\theta)$ where Z is the normalization constant and $\theta$ is a parameter characterizing the equilibrium between two systems in contact, playing the same role than temperature in Classical Statical Mechanics Notice that the separability property of G in Volterra's model is an exact property, not being necessary to assume the existence of a small G' taking care of the interaction between species, unlike what happens with the hamiltonian of an ideal system of particles. In the Volterra model, the fact that G is of the form given by Eq. (2) does not mean that the species do not interact.

The average value of the function $f(x_1,\ldots,x_n)$ can be found using the expression

$$<f(x_1,\ldots,x_n)> = \frac{\int dx_1\ldots dx_n \rho(x_1,\ldots,x_n) f(x_1,\ldots,x_n)}{\int dx_1\ldots dx_n \rho(x_1,\ldots,x_n)} \qquad (3)$$

Within the canonical ensemble (used by Kerner) we obtain

$$< x_i \frac{\partial G}{\partial x_i} > = \theta \qquad (4)$$

This result is analogous to the equipartition theorem in Classical Statistical Mechanics. It shows up the meaning of $\theta$ for a biological association. For the two interacting species case and using the facts that G is a constant of motion and that the variables $x_1, x_2$ verify Liouville's theorem, it is easy to prove that $\dot{x}_1 = \partial G/\partial x_2$ and $\dot{x}_2 = -\partial G/\partial x_1$ (notice the formal analogy with Hamilton's equations). Hence

$$< x_1\dot{x}_2 > = -< x_2\dot{x}_1 > = \theta \qquad (5)$$

The meaning of $\theta$ can be understood by evaluating the average value of $(\partial G/\partial x_i)^2$. The result shows that $\theta$ measures the mean square deviation of each of the populations from their stationary values. For $\theta = 0$, the biological association is in a stationary state, completely "quite". The moments of order p of the variables $N_1$ and $N_2$ are given by

$$<N_1^p> = q_1^p \frac{\Gamma(p + a_2/\theta)}{\Gamma(a_2/\theta)(a_2/\theta)^p} \qquad (6a)$$

$$<N_2^p> = q_2^p \frac{\Gamma(p + a_1/\theta)}{\Gamma(a_1/\theta)(a_1/\theta)^p} \qquad (6b)$$

where $q_1 \equiv a_2/b_2$ and $q_2 \equiv a_1/b_1$, are the stationary values of the system (1) and $\Gamma$ represents Euler's gamma function. For $\theta \to 0$ we obtain $<N_i^p> = <N_i>^p$ which ensures the non-existence of fluctuations in that limit.

Using this procedure, Kerner found several equipartition theorems, suitable for experimental verification; a "heat" flux theorem (this quantity is conserved for an isolated association) between two weakly coupled associations with different temperatures; a Dulong and Petit's law for the heat capacity; a law similar to the second law of Thermodynamics (expressing the tendency of an association towards a maximum entropy equilibrium state); an equation of state, etc... Therefore, Kerner's theory leads to a thermodynamical formulation of the biological association although we do not have an adequate experimental reference frame (R.M. May, 1974).

## III. General theory.-

In this section we investigate under what conditions a system of two coupled differential equations can be treated by Kerner's statistical mechanical method. As we mentioned above, the two requirements are the existence of a constant of the motion and the verification of a Liouville theorem in some phase space.

Let us start with the most general form of the equations of motion

$$\dot{N}_1 = \psi_1(N_1,N_2) \qquad (7a)$$

$$\dot{N}_2 = \psi_2(N_1,N_2) \qquad (7b)$$

where $\psi_1$ and $\psi_2$ are arbitrary functions of $N_1$ and $N_2$. Let us assume that a constant of motion G exists. Then $\dot{G}(N_1,N_2) = 0$, or more explicitly

$$\frac{\partial G}{\partial N_1}\dot{N}_1 + \frac{\partial G}{\partial N_2}\dot{N}_2 = \frac{\partial G}{\partial N_1}\psi_1(N_1,N_2) + \frac{\partial G}{\partial N_2}\psi_2(N_1,N_2) = 0 \qquad (8)$$

The constants of the motion are the solutions of this linear and homogeneous first order partial differential equation. According to the theorem for the existence and the uniqueness of partial differential equations (Elsgoltz, 1969), we can find a solution of Eq. (8) if $\psi_1(N_1,N_2)$ and $\psi_2(N_1,N_2)$ are continuous functions such that they do not vanish simultaneously in any point of the region $0 < N_i < \infty$ and their partial derivatives exist in that region. In this case, the solution of (8) is obtained from the solution of

$$\frac{d\,N_1}{\psi_1(N_1,N_2)} = \frac{d\,N_2}{\psi_2(N_1,N_2)} \qquad (9)$$

If the solution of Eq. (9) is given by the characteristic curves $\phi(N_1,N_2) = C$, the general solution of Eq. (8) is then $G = \Phi[\phi(N_1,N_2)]$ where $\Phi$ is some arbitrary function.

On the other hand, Eqs. (7) must satisfy Liouville's theorem. This leads us to define new variables.

In fact, it is easy to see that in the phase space defined by $N_1$ and $N_2$, Liouville's theorem is verified just if $\dot{N}_1$ depends only on $N_2$, and $\dot{N}_2$ depends only on $N_1$, and that is a very particular situation. We, thus change to a new set of variables

$$x_1 = f_1\,(N_1,N_2) \tag{10a}$$

$$x_2 = f_2\,(N_1,N_2) \tag{10b}$$

We want $\partial\dot{x}_i/\partial x_i = 0$ to be satisfied. Taking the time derivative of $x_1$ and using Eqs. (7) we find

$$\dot{x}_1=\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}\dot{N}_1+\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1}\dot{N}_2=\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}\psi_1+\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1}\psi_2 \tag{11}$$

On the other hand, we can write

$$\left(\frac{\partial \dot{x}_1}{\partial x_1}\right)_{x_2} = \left(\frac{\partial \dot{x}_1}{\partial N_1}\right)_{N_2}\left(\frac{\partial N_1}{\partial x_1}\right)_{x_2} + \left(\frac{\partial \dot{x}_1}{\partial N_2}\right)_{N_1}\left(\frac{\partial N_2}{\partial x_1}\right)_{x_2} \tag{12}$$

Let us now write Eq. (12) in terms of the f's and $\psi$'s To do so, let us take the partial derivative of Eq. (11) with respect to $N_1$ keeping $N_2$ constant and vice-versa.

$$\left(\frac{\partial \dot{x}_1}{\partial N_1}\right)_{N_2}=\left(\frac{\partial^2 f_1}{\partial N_1^2}\right)_{N_2}\psi_1+\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}\left(\frac{\partial \psi_1}{\partial N_1}\right)_{N_2}+\frac{\partial^2 f_1}{\partial N_1\partial N_2}\psi_2 + \left(\frac{\partial f_1}{\partial N_2}\right)_{N_1}\left(\frac{\partial \psi_2}{\partial N_1}\right)_{N_2} \tag{13a}$$

$$\left(\frac{\partial \dot{x}_1}{\partial N_2}\right)_{N_1}=\frac{\partial^2 f_1}{\partial N_2\partial N_1}\psi_1+\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}\left(\frac{\partial \psi_1}{\partial N_2}\right)_{N_1}+\left(\frac{\partial^2 f_1}{\partial N_2^2}\right)_{N_1}\psi_2 + \left(\frac{\partial f_1}{\partial N_2}\right)_{N_1}\left(\frac{\partial \psi_2}{\partial N_2}\right)_{N_1} \tag{13b}$$

Then using the identity

$$\left(\frac{\partial x_1}{\partial N_1}\right)_{x_2} = \left(\frac{\partial x_1}{\partial N_1}\right)_{N_2} + \left(\frac{\partial x_1}{\partial N_2}\right)_{N_1}\left(\frac{\partial N_2}{\partial N_1}\right)_{x_2} =$$

$$= \left(\frac{\partial x_1}{\partial N_1}\right)_{N_2} - \left(\frac{\partial x_1}{\partial N_2}\right)_{N_1}\frac{(\partial x_2/\partial N_1)_{N_2}}{(\partial x_2/\partial N_2)_{N_1}}$$

$$=\left[\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1}\right]^{-1}\left[\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1} - \left(\frac{\partial f_1}{\partial N_2}\right)_{N_1}\left(\frac{\partial f_2}{\partial N_1}\right)_{N_2}\right] \tag{14}$$

we obtain

$$\left(\frac{\partial N_1}{\partial x_1}\right)_{x_2}=\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1}\left[\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1}-\left(\frac{\partial f_1}{\partial N_2}\right)_{N_1}\left(\frac{\partial f_2}{\partial N_1}\right)_{N_2}\right]^{-1} \tag{15a}$$

$$\left(\frac{\partial N_2}{\partial x_1}\right)_{x_2}=-\left(\frac{\partial f_2}{\partial N_1}\right)_{N_2}\left[\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1}-\left(\frac{\partial f_1}{\partial N_2}\right)_{N_1}\left(\frac{\partial f_2}{\partial N_1}\right)_{N_2}\right]^{-1} \tag{15b}$$

Therefore, if we want Liouville's theorem $\left(\frac{\partial \dot{x}_1}{\partial x_1} = \frac{\partial \dot{x}_2}{\partial x_2} = 0\right)$ to be satisfied, the functions $f_1$ and $f_2$ must verify the following system of second order coupled partial differential equations

$$\left[\left(\frac{\partial^2 f_1}{\partial N_1^2}\right)_{N_2}\psi_1+\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}\left(\frac{\partial \psi_1}{\partial N_1}\right)_{N_2}+\frac{\partial^2 f_1}{\partial N_1\partial N_2}\psi_2+\left(\frac{\partial f_1}{\partial N_2}\right)_{N_1}\left(\frac{\partial \psi_2}{\partial N_1}\right)_{N_2}\right]\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1}$$

$$= \left[\frac{\partial^2 f_1}{\partial N_1\partial N_2}\psi_1+\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}\left(\frac{\partial \psi_1}{\partial N_2}\right)_{N_1}+\left(\frac{\partial^2 f_1}{\partial N_2^2}\right)_{N_1}\psi_2+\left(\frac{\partial f_1}{\partial N_2}\right)_{N_1}\left(\frac{\partial \psi_2}{\partial N_2}\right)_{N_1}\right]\left(\frac{\partial f_2}{\partial N_1}\right)_{N_2} \tag{16a}$$

$$\left[\left(\frac{\partial^2 f_2}{\partial N_2^2}\right)_{N_1}\psi_2+\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1}\left(\frac{\partial \psi_2}{\partial N_2}\right)_{N_1}+\frac{\partial^2 f_2}{\partial N_2\partial N_1}\psi_1+\left(\frac{\partial f_2}{\partial N_1}\right)_{N_2}\left(\frac{\partial \psi_1}{\partial N_2}\right)_{N_1}\right]\left(\frac{\partial f_1}{\partial N_1}\right)_{N_2}$$

$$= \left[\frac{\partial^2 f_2}{\partial N_2\partial N_1}\psi_2+\left(\frac{\partial f_2}{\partial N_2}\right)_{N_1}\left(\frac{\partial \psi_2}{\partial N_1}\right)_{N_2}+\left(\frac{\partial^2 f_2}{\partial N_1^2}\right)_{N_2}\psi_1+\left(\frac{\partial f_2}{\partial N_1}\right)_{N_2}\left(\frac{\partial \psi_1}{\partial N_1}\right)_{N_2}\right]\left(\frac{\partial f_1}{\partial N_2}\right)_{N_1} \tag{16b}$$

Solving (16) is not an easy task. Furthermore, even if we are able to find a solution in some particular case, that solution might be not very useful, because it could lead to a very sophisticated change of variables and to a very difficult interpretation of the average values. Let us restrict ourselves, then, to a particularly simple case, although probably there are some other cases that could be analized in a simple fashion. Let us admit that $f_1$ and $f_2$ satisfy

$$\left(\frac{\partial f_1}{\partial N_2}\right)_{N_1} =\left(\frac{\partial f_2}{\partial N_1}\right)_{N_2} = 0 \tag{17}$$

The system (16) takes the form

$$\frac{d^2 f_1}{d N_1^2}\psi_1 + \frac{df_1}{dN_1}\left(\frac{\partial \psi_1}{\partial N_1}\right)_{N_2} = 0 \tag{18a}$$

$$\frac{d^2 f_2}{d N_2^2}\psi_2 + \frac{df_2}{dN_2}\left(\frac{\partial \psi_2}{\partial N_2}\right)_{N_1} = 0 \tag{18b}$$

and from here we obtain

$$\frac{d \log f_1'}{d N_1} = - \left(\frac{\partial \log \psi_1}{\partial N_1}\right)_{N_2} \tag{19}$$

where $f_1' \equiv df_1/dN_1$. Taking the derivative with respect to $N_2$,

$$\frac{\partial^2 \log \psi_1}{\partial N_2 \partial N_1} = 0$$

This last result indicates that $\psi_1$ (and also $\psi_2$) must factorize in the form

$$\psi_1(N_1,N_2) = - A_1(N_1)\, B_2(N_2) \qquad (20a)$$

$$\psi_2(N_1,N_2) = A_2(N_2)\, B_1(N_1) \qquad (20b)$$

where the minus sign in (20a) has been introduced for convenience. Solving Eq. (19) we obtain the change of variables

$$f_1(N_1) = C_1 \int \frac{dN_1}{A_1(N_1)} \qquad (21a)$$

$$f_2(N_2) = C_2 \int \frac{dN_2}{A_2(N_2)} \qquad (21b)$$

where $C_1$ and $C_2$ are some arbitrary constants.

Now, the constant of the motion can be easily obtained. Substitution of Eqs. (20) into Eqs. (7) leads to

$$[B_1(N_1)/A_1(N_1)]\, \dot{N}_1 = -B_1(N_1)\, B_2(N_2) \qquad (22a)$$

$$[B_2(N_2)/A_2(N_2)]\, \dot{N}_2 = B_2(N_2) B_1(N_1) \qquad (22b)$$

and hence

$$\frac{B_1(N_1)}{A_1(N_1)}\dot{N}_1 + \frac{B_2(N_2)}{A_2(N_2)}\dot{N}_2 = 0 \qquad (23)$$

The integration of Eq. (23) directly provides the constant of the motion

$$G(N_1,N_2) = \int dN_1 \frac{B_1(N_1)}{A_1(N_1)} + \int dN_2 \frac{B_2(N_2)}{A_2(N_2)} = G_1(N_1)+G_2(N_2) \qquad (24)$$

We can also arrive to the same result by solving Eq. (9).

Table 1

| MODELS | | $A_1(N_1)$ | $B_2(N_2)$ | $A_2(N_2)$ | $B_1(N_1)$ |
|---|---|---|---|---|---|
| 1 VOLTERRA | $\dot{N}_1=N_1(a_1-b_1N_2)$<br>$\dot{N}_2=-N_2(a_2-b_2N_1)$ | $N_1$ | $b_1N_2-a_1$ | $N_2$ | $b_2N_1-a_2$ |
| 2 POWER | $\dot{N}_1=N_1(a_1-b_1N_2^n)$<br>$\dot{N}_2=-N_2(a_2-b_2N_1^m)$ | $N_1$ | $b_1N_2^n-a_1$ | $N_2$ | $b_2N_1^m-a_2$ |
| 3 LOGARITHMIC | $\dot{N}_1=N_1(a_1-b_1\log N_2)$<br>$\dot{N}_2=-N_2(a_2-b_2\log N_1)$ | $N_1$ | $b_1\log N_2-a_1$ | $N_2$ | $b_2\log N_1-a$ |
| 4 SATURATION | $\dot{N}_1=N_1(a_1-b_1\frac{N_2}{N_2+D})$<br>$\dot{N}_2=-N_2(a_2-b_2N_1)$ | $N_1$ | $b_1\frac{N_2}{N_2+D}-a_1$ | $N_2$ | $b_2N_1-a_2$ |
| 5 PLANT-HERBIVORE | $\dot{N}_1=a_1-b_1N_2$<br>$\dot{N}_2=a_2N_2(1-\frac{b_2N_2}{a_1})$ | 1 | $b_1N_2-a_1$ | $N_2(1-\frac{b_2N_2}{a_1})$ | $a_2$ |
| 6 COWAN | $\dot{N}_1=(a_1-b_1N_2)N_1(1-N_1)$<br>$\dot{N}_2=-(a_2-b_2N_1)N_2(1-N_2)$ | $N_1(N_1-1)$ | $a_1-b_1N_2$ | $N_2(N_2-1)$ | $a_2-b_2N_1$ |
| 7 GOODWIN | $\dot{N}_1=\frac{a_1-b_1N_2}{A_1+k_1N_2}$<br>$\dot{N}_2=-(a_2-b_2N_1)$ | 1 | $\frac{b_1N_2-a_1}{A_1+k_1N_2}$ | 1 | $b_2N_1-a_2$ |

TABLE 2:

| MODELS | $\langle N_1^p\rangle$ | $\langle N_1\rangle$ | $\langle N_2^s\rangle$ | $\langle N_2\rangle$ |
|---|---|---|---|---|
| 1 VOLTERRA | $q_1^p \frac{\Gamma(p+a_2/\theta)}{\Gamma(a_2/\theta)(a_2/\theta)^p}$ | $q_1$ | $q_2^s \frac{\Gamma(s+a_1/\theta)}{\Gamma(a_1/\theta)(a_1/\theta)^s}$ | $q_2$ |
| 2 POWER | $q_1^p \frac{\Gamma(p/m+a_2/m\theta)}{\Gamma(a_2/m\theta)(a_2/m\theta)^{p/m}}$ | $q_1 \frac{\Gamma(1/m+a_2/m\theta)}{\Gamma(a_2/m\theta)(a_2/m\theta)^{1/m}}$ | $q_2^s \frac{\Gamma(s/n+a_1/n\theta)}{\Gamma(a_1/n\theta)(a_1/n\theta)^{s/n}}$ | $q_2 \frac{\Gamma(1/n+a_1/n\theta)}{\Gamma(a_1/n\theta)(a_1/n\theta)^{1/n}}$ |
| 3 LOGARITHMIC | $q_1^p \exp(\theta p^2/2b_2)$ | $q_1 \exp(\theta/2b_2)$ | $q_2^s \exp(\theta s^2/2b_1)$ | $q_2 \exp(\theta/2b_1)$ |
| 4 SATURATION | $q_1^p \prod_{n=1}^{p} [1+(n-1)\theta/a_2]$ | $q_1$ | $q_2^s \prod_{n=1}^{s} \frac{1+(n-1)\theta/a_1}{1-n\theta/(b_1-a_1)}$ | $\frac{q_2}{1-\theta/(b_1-a_1)}$ |
| 5 PLANT-HERBIVORE | $p!\,(\theta/a_2)^p$ | $\theta/a_2$ | $q_2^s$ | $q_2$ |
| 6 COWAN | $q_1^p \prod_{n=1}^{p} \frac{a_2+(p-n)\theta}{a_2+(p-n)q_1\theta}$ | $q_1$ | $q_2^s \prod_{n=1}^{s} \frac{a_1+(s-n)\theta}{a_1+(s-n)q_2\theta}$ | $q_2$ |
| 7 GOODWIN | $q_1^p \pi^{-1/2} \sum_{n=0}^{p} \binom{p}{n} (2\theta/q_1a_2)^{n/2}\Gamma(\frac{n+1}{2})$ | $q_1+(2\theta/\pi b_2)^{1/2}$ | $q_2^s \sum_{n=0}^{s} \binom{s}{n} (-A_1/k_1q_2)^{s-n}(1+A_1/k_1q_2)^n \alpha_n$ <br> $\alpha_n = \prod_{m=0}^{n} [1+\frac{m\,k_1\,\theta}{a_1(1+A_1/k_1q_2)}]$ | $q_2 + \theta k_1/b_1$ |

We then have identified the constant of the motion and the new variables defining a phase space, where a Liouville theorem is verified, if the conditions (20) are satisfied. Otherwise, the system (16) has to be solved.

Note that we find again the additivity property (24) that we already found in Volterra's model.

## IV. Aplication to some particular models.-

In this section we present a brief description of some biological models described by the general theory. Table 1 shows the system of equations defining them and the expressions for the corresponding arbitrary functions introduced in Eqs. (20).

Models 2, 3 and 4 represent modifications of Volterra's model. Keeping the same structure as in Volterra's model we can think about modifying the functions characterizing the interaction term. The power and logarithmic laws are particularly attractive and do not alter the interpretation of the model. The difference with the Volterra's model lies only on the strength of the interaction between species. Another possibility is to introduce an interaction term with some asymptotic limit, namely, a function that gives rises to a kind of "saturation". The saturation model in Table 1 is suggested by analogous models discussed by R.M. May (1976).

The plant-herbivore model (G. Caughley, 1976) is used in ecological studies. $N_1$ represents the vegetation and $N_2$ the herbivorous population. The rate of renewal of plants, $a_1$, is affected by the presence of animals whose population increase in counterbalanced by a term of self-regulation that depends inversely on $a_1$.

The last two models are not ecological ones, though they also admit a statistical mechanical treatment. Cowan's model (1968) describes the activity of the central nervous system due to interactions inside each nervous network and among them. Finally, Goodwin's biochemical model (1963, 1970) describes control equations for the protein synthesis..

The results obtained for the different models are presented in Table 2 where $q_i$ represent the stationary values of $N_i$. In the plant-herbivore model, $N_2$, the number of herbivores, has two stationary values: $q_2$ (corresponding to $N_2 = 0$), and $q_2'$ (corresponding to $N_1 = 0$), such that $q_2' > q_2$. Besides, there is not any stationary value for $N_1$.

The moments of the distributions for each population are also given in Table 2. From those values, we can find expressions for the average values of arbitrary functions of $N_i$, using a series expansion. In the low temperature limit $\theta \to 0$ we find $\langle N_i^p \rangle = \langle N_i \rangle^p$, namely, there are not fluctuations around the average values and the number of individuals is constant in all the systems forming the ensemble. An exception of this result occurs in the plant-herbivore model where $\langle N_1^p \rangle = p! \langle N_1 \rangle^p$ for any value of $\theta$. In particular for p=2 we have $[\langle N_1^2 \rangle - \langle N_1 \rangle^2]/\langle N_1 \rangle^2 = 1$. In other words, the fluctuations of the amount of vegetation around its average value is of the same order of magnitude as its average value. Therefore, in the limit $\theta \to 0$ the fluctuations do not decrease relative to the averages; both the average value and the fluctuations go to zero in the same way when $\theta \to 0$. Furthermore, the herbivore population does not fluctuate for any value of $\theta$.

Let us also notice that the average value of each population does not in general coincide with the stationary value. This follows from the fact that the statistical variable is not always $N_i$, but a given function of $N_i$.

The system of equations defining the plant-herbivore model has an exact solution $N_1(t)$ and $N_2(t)$. It is evident that a deterministic interpretation of this solution is meaningless. In our treatment, where the equations represent the motion of microstates, expressions for the fluctuations around average values are obtained.

Due to the special form $\dot{N}_2(N_2)$ of the equation of motion for the herbivore, the change of variables suitable for the verification of Liouville's theorem is a linear function of time. Finally, let us notice that in Goodwin's model the new variable is $N_i$, because the equations of motion written in terms of $N_i$, already allow the verification of a Liouville theorem

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