FURTHER CONSIDERATIONS ON THE STATISTICAL
MECHANICS OF BIOLOGICAL ASSOCIATIONS

EDWARD H. KERNER*
PHYSICS DEPARTMENT
UNIVERSITY OF BUFFALO

In this continuation of a previous report it is shown how the Volterra population dynamics, which underlies the statistical theory, can be based on a variational principle; how the dynamics can be generalized as regards both the behavior of total populations and migration phenomena; and how many directly observable data, such as amplitudes and frequencies of oscillation of a population, fit into the statistical theory and can test it. Such a test is carried out in some detail using the fox-catch data of Elton, with a clear indication that the theory is capable of comprehending the major statistical properties of population-time curves. A final section sketches an extension of the theory to cover secular variations of external conditions such as temperature of the environment.

1. *Introduction.* In a previous report (Kerner, 1957) it was shown that the classical Volterra equations, which provide a general, if somewhat oversimplified, dynamics of interacting species, lend themselves to a statistical, or thermodynamic, type of analysis comparable to that used for physical systems having a great many degrees of freedom (when the number of species is too large to allow any detailed description of the individual population variations). The analysis led to a number of experimentally verifiable or deniable consequences and contained an unforced statement of an important proposition in mathematical ecology, founded on observation in the field, due to Corbet, Fisher, and Williams.

The present note aims to amplify the prior one. First, some general remarks on the Volterra equations will be made, and a pro-

posal advanced to remedy the serious omission, in the Volterra
theory and in other demographic theories, of an account of popula-
tion variations in *space* as well as time. Then it will be shown
how the numerical parameters entering the Volterra equations—
which play the role of "microscopic" parameters in the thermo-
dynamic view, much as atomic masses are the microscopic con-
stants of gas theory—may be fairly directly observed within the
large biological ensemble and not through the practically impos-
sible observation of isolated pairs of interacting species. Next
comes a demonstration of how some types of statistical data on
selected populations, principally amplitudes and frequencies of
oscillation of populations, fit into the thermodynamic scheme and
constitute tests for it.

Following this is an actual, if somewhat rough, test of several
theoretical conclusions against ecological field data.

Throughout, our tool will be the Gibbs canonical ensemble to-
gether with the assumption of ergodicity: *time averages = ensemble
averages*. The main viewpoint is that the oscillating populations
of some few out of a great many interlocking species are among the
primary ecologic observables that must be fitted into a general
scheme. The question is, What do such population data mean?
What elements in the data are not simply of empirical interest but
are predictable and co-related? What, after all, is there to be
learned from a population-time curve looking like an overblown
picture of random noise? The statistical Volterra mechanics gives
some clear and comprehensive set of answers *a priori*. If the an-
swers are not correct, one has at least something definite to rebut
and perhaps a point of departure for better theorizing.

In the concluding section there will be discussed briefly the
non-stationary ensembles suited to the study of quasi-static alter-
ations of external variables (such as physical temperature) affect-
ing biological associations.

2. *Generalities on the Volterra mechanics.* Volterra's (1931,
1937) theory of interacting populations is essentially constituted
by the system of differential equations,

$$\frac{dN_r}{dt} = \epsilon_r N_r + \frac{1}{\beta_r} \sum_s \alpha_{sr} N_s N_r , \tag{1}$$

for the population numbers N of the coupled species, with $\alpha_{sr} = -\alpha_{rs}$. Introducing the stationary state $dN_r/dt = 0$ as in the earlier report and again calling q_r the stationary population levels satisfying

$$\epsilon_r \beta_r + \sum_s \alpha_{sr} N_s = 0, \qquad (2)$$

we have shown that equation (1) may be cast in the form

$$\dot{v}_r = \sum_s \gamma_{sr} \frac{\partial G}{\partial v_s} \qquad (3)$$

with

$$v_r \equiv \log \frac{N_r}{q_r}; \quad \gamma_{sr} \equiv \frac{\alpha_{sr}}{\beta_s \beta_r} = -\gamma_{rs};$$

$$G \equiv \Sigma \; r_r \, (e^{v_r} - v_r); \quad (r_r \equiv q_r \beta_r).$$

As previously, it will be assumed that equations (2) have unique, positive solutions and hence that there is an even number of species in association and that not all ϵ are of like sign. The quantity G is a constant of the motion holding the cardinal position in the present thermodynamic development that the Hamiltonian holds in the analogous physical problem.

We should like to show that equations (3) are comprehended under a variational principle similar to Hamilton's principle in mechanics. This should not be confused with Volterra's (1937) variational principle for equations (1), which hinges on the clumsy artifice of writing these equations as *second-order* equations in the variables $X_r = \int N_r \, at$.

Consider the function

$$\Lambda = \frac{1}{2} \sum_i \sum_j \Gamma_{ij} v_i \dot{v}_j - G,$$

where the matrix of Γ_{ij} is antisymmetric and non-singular (therefore, of even order) but otherwise unspecified for the moment. The vanishing of the variation of the time-integral of Λ, with fixed endpoints, i.e.,

$$\delta \int_{t_1}^{t_2} \Lambda\, dt = 0, \tag{4}$$

occurs just when the v's satisfy the Euler-Lagrange equations

$$\frac{d}{dt}\frac{\partial \Lambda}{\partial \dot{v}_k} - \frac{\partial \Lambda}{\partial v_k} = 0,$$

or, explicitly,

$$\frac{1}{2}\sum_i \Gamma_{ik}\,\dot{v}_i - \frac{1}{2}\sum_j \Gamma_{kj}\,\dot{v}_j + \frac{\partial G}{\partial v_k} = 0.$$

Replacing Γ_{ik} by $-\Gamma_{ki}$, and then the dummy index i by the equally dummy j, this says

$$\sum_j \Gamma_{kj}\,\dot{v}_j = \frac{\partial G}{\partial v_k}.$$

Let us invert this set of equations, solving for $\dot{v}_r$:

$$\dot{v} = \sum_s (\Gamma^{-1})_{rs}\frac{\partial G}{\partial v_s}. \tag{5}$$

Now if Γ is antisymmetric, so also is Γ^{-1}; for $(\Gamma^{-1})_{rs} \sim (s, r\ \text{minor}$ of $\Gamma)$, and if rows and columns of this minor are interchanged, one

gets a determinant, D, identical with the r, s minor, Δ, except that its elements have indices the reverse of those of Δ; hence, if these indices in D are indeed reversed, one gets $(-1)D$ coming to be the same as Δ, since the order of D is *odd*.

Thus equations (5), which are equations (3) with γ_{sr} disguised as $(\Gamma^{-1})_{rs}$, are summarized in the "least-action" type of variational principle of equation (4). Not only is $\int \Lambda dt$ stationary about (5) for first-order variations in the v's; it is also stationary to the second order of varied v's. We have, in fact, calculating the variation of the "action" to the second order,

$$\delta \int \Lambda dt = \int \frac{1}{2} \sum \sum \Gamma_{ij} \, v_i \, \delta \dot{v}_j + (\delta v_i) \, \dot{v}_j - \sum \frac{\partial G}{\partial v_i} \delta v_i +$$

$$\int \frac{1}{2} \sum \sum \Gamma_{ij} \, \delta v_i \, \delta \dot{v}_j - \frac{1}{2} \sum \sum \frac{\partial^2 G}{\partial v_i \, \partial v_j} \delta v_i \delta v_j.$$

The first integral on the right vanishes, as above, just if (5) holds. The second similarly vanishes upon writing the first member of the integrand as

$$\frac{1}{2} \sum \sum \Gamma_{ij} \, \delta v_i \, \delta \dot{v}_j = \frac{1}{2} \sum_i \sum_j \sum_k \sum_l \Gamma_{ij} \, (\Gamma^{-1})_{jk} \frac{\partial^2 G}{\partial v_k \, \partial v_l} \delta v_l \, \delta v_i =$$

$$\frac{1}{2} \sum_i \sum_k \sum_l \delta_{ik} \frac{\partial^2 G}{\partial v_k \, \partial v_l} \delta v_l \, \delta v_i = \frac{1}{2} \sum_k \sum_l \frac{\partial^2 G}{\partial v_k \, \partial v_l} \delta v_l \, \delta v_k,$$

which cancels the second member identically.

Following formally for a moment a classic pattern, the "momentum" conjugate to the "coordinate" v_k is

$$p_k \equiv \frac{\partial \Lambda}{\partial \dot{v}_k} = \frac{1}{2} \sum_i \Gamma_{ik} \, v_i,$$

and the "Hamiltonian" is

$$\sum p_k \, \dot{v}_k - \Lambda = \frac{1}{2} \sum \sum \Gamma_{ik} \, v_i \, \dot{v}_k - \frac{1}{2} \sum \sum \Gamma_{ij} \, v_i \, \dot{v}_j + G = G.$$

While in a purely formal sense G may therefore be looked upon as a Hamiltonian, it must be recognised that the whole Hamiltonian procedure of dynamics is here nugatory, owing to the fact that, to begin with, the "Lagrangian" equations $\dot{p}_k = \partial \Lambda / \partial v_k$ are of the first order.

Turning now to a different matter, it will have been observed that no use has been made of any particular form for the primary integral, G, of the system (3). This invites some comments on generalizations of the Volterra scheme.

Let us hold to the aim of preserving a basic conservation law, which in any subsequent statistical mechanics would be of fundamental importance. Volterra, in his 1931 monograph, had already extended his original equations (1) to embrace the wider type of conservation, $\Sigma \, \psi_i(N_i) = const$, for nearly arbitrary ψ, of which

$$\sum G_i = \sum r_r (e^{v_r} - v_r) = \sum r_r \left(\frac{N_r}{q_r} - \log \frac{N_r}{q_r} \right) \tag{6}$$

(referring just to the original equations) is but a particular example.

It is clear, however, from the standpoint of equations (3) that an appreciably more general type of conservation than Volterra's is at hand. Thus, adhering only to the antisymmetry of the γ_{rs}—engendered initially by the idea of reciprocal binary interactions between species but now not necessarily limited in meaning by this concept—it is seen that $G(v_1, v_2, \ldots, v_n) = constant$, irrespective of both the functional dependence of G on the v and, of course, of the dependence of the v on the population numbers N. Volterra conservation, in this view, is simply the special choice $G = \Sigma \, G_i(v_i)$, $v_i = v_i(N_i)$. The γ_{rs} here, of course, need not be constants but may be functions of the dependent variables v.

We may note in passing a characteristic time-reversal symmetry of equations (3), namely, that if $t \rightarrow (-t)$, the equations are unchanged if also the signs of all γ_{rs} are reversed, meaning in the

original usage ($\gamma_{rs} = \alpha_{rs}/\beta_r\beta_s$) a reversal of the roles of predator and prey, thus a kind of biologic analog to the principle of dynamic reversibility. The existence of the integral G reflects this symmetry in a manner akin to energy-conservation's mirroring the time-symmetry of Newton's mechanics.

It is well to remember at this point the original purpose of having transferred from N-space to the more abstract v-space: it was to make v-space a satisfactory phase space in which Liouville's theorem holds and Gibbs ensembles may be studied. Sufficient and necessary for the Gibbs statistical mechanics are a mechanics, equations (3), admitting a Liouville theorem and a suitable constant of the motion, plus great ignorance otherwise. Let us see about Liouville's theorem in the context of the generalization of Volterra, the other requirements having been met. For a Gibbs ensemble of phase points in v-space, the equation of continuity is

$$\frac{\partial \rho}{\partial t} + \text{div } \rho \underline{V} = 0,$$

ρ being the density, $\underline{V}$ the velocity of phase points, reckoned as point-functions in the space. Expanding the divergence,

$$\frac{\partial \rho}{\partial t} + \underline{V} \cdot \nabla \rho + \rho \text{ div } \underline{V} = \frac{D\rho}{Dt} + \rho \text{ div } \underline{V} = 0.$$

We can have Liouville's theorem, $D\rho/Dt = 0$, just if div $\underline{V} = 0$:

$$\sum \frac{\partial \dot{v}_r}{\partial v_r} = \sum \sum \frac{\partial \gamma_{sr}}{\partial v_r} \frac{\partial G}{\partial v_s} + \gamma_{sr} \frac{\partial^2 G}{\partial v_r \partial v_s}$$

$$= \sum \sum \frac{\partial \gamma_{sr}}{\partial v_r} \frac{\partial G}{\partial v_s} = 0.$$

This may be counted as a condition on the γ or G or both. It is seen to be not strongly restrictive; for example, it suffices that, with arbitrary G, $\gamma_{rs}(v_1, v_2, \ldots, v_n)$ be independent of v_r and v_s.

The position altogether is that the Volterra scheme may be substantially broadened, and without harm to statistical mechanization. In illustration of the possible utility of the extra breadth, note that the canonical distribution retains the form

$$\rho = e^{\frac{\psi - G}{\theta}}.$$

Previously, G was fixed as in equation (6) and so gave us a density-in-phase, in which the components $G_r(v_r)$ were strictly separated, so that the probability densities for the separate species were independent and of the form (returning to N-space)

$$P(n_r) \, dn_r \sim n_r^{x_r - 1} \, e^{-x_r n_r} \, dn_r \tag{7}$$

($n_r = N_r/q_r$; $x_r = r/\theta$; $\theta = $ "temperature" of the association). Now, however, we may reject the independence by writing, for instance, $G = \Sigma \Sigma \, g_r(v_r) \, h_s(v_s)$ and $v_s = v_s(N_s)$, or $G = \Sigma \, G_i(v_i)$ and $v_i = v_i(N_1, \ldots, N_n)$; or we may keep the independence (very convenient mathematically), $G = \Sigma \, G_i(v_i)$ and $v_i = v_i(N_i)$, such as to give any desired form to the probability law of type (7), according to what may be dictated by observational experience. This is to say— under the circumstances of observation in the field, where it is practically out of the question to discern directly whatever micromechanics is actuating the population fluctuations but rather where probability statements like (7) are in the offing—that one may possibly glean a clue to the mechanics from just such statements, and having the mechanics is to have a basis for suggestions as to further observations and otherwise unforeseen connections among them. Naturally, it cannot be expected that the whole mechanics is inferrable from the statistics alone; and it is certainly arguable, to begin with, that a differential mechanics can hold in any strict sense, though differential equations have had a value in the past and are apt to be useful for some time to come. The point is that the sense need not be so strict in the light of the coarseness of the observations; a statistical mechanics stemming from a crude mechanics may well be sufficient for the data and for the prediction of data. "A tous ces developpements théoriques, quelles con-

firmation l'expérience va-t-elle? Les *vérifications expérimentales* sont à peine commencées"; this holds nearly as truly now as it did in 1931.

For the present we shall keep to the original Volterra scheme because it contains the result (7) having observational basis; because it proceeds from reasonable, if simplified, *a priori* considerations; and because it is relatively tractable mathematically.

3. *Hint to a theory of migration: migration as a generalised diffusion process.* Many demographic theories eschew a space-time description of populations, confining their attention principally to time-variations of population numbers. We should like here to sketch a few ideas which may give some account in general terms of migrational, as well as temporal, behavior; the ideas are not all novel qualitatively, but perhaps their quantitative exposition here may be. This stands as something of a digression from the statistical-mechanical discussion (as yet) but seems close enough to our previous general ecological considerations to warrant presentation in this place.

The basic assumption is that, looking at a number of species distributed over a large region of space, it is possible to select much smaller regions $\Delta r = \Delta x \Delta y \Delta z$ containing ΔN_i individuals of species i such that $\Delta N_i / \Delta r$ may be sensibly reckoned on an appropriate scale of length as a scalar point function, the population density $\rho_i(r, t)$ of the ith species (r denotes generic position x, y, z in space). Since the organisms comprising each species are generally in motion of one sort or another, we also introduce the current density, $j_i(r, t)$, such that the net number of i's per unit time crossing the small area ΔS, having unit normal vector $\hat{n}$, is $j \cdot \hat{n} \Delta S$. In other words, the view is that of the bacteriologist looking at a broth by eye or through the low-power microscope or of the aviator scanning in some perspective the field life below from his high perch.

It is barely more than a truism now to write an equation of continuity: let V be a large enough volume bounded by the surface S, and R_i the net rate of increase, per unit volume and per unit time, of species i due to its self-propagation and interaction with other species. Then ($\hat{n}$ denoting the *outward* normal to S)

$$\frac{\partial}{\partial t} \int_V \rho_i \, d\tau = \int_S j_i \cdot (-\hat{n}) \, dS + \int_V R_i \, d\tau, \qquad (8)$$

or

(net rate of increase in = (net rate of   + (natural rate of
  V of species i)   immigration   increase within
                                       into V through V, exclusive of
                                       S)   immigration).

Upon using Gauss's law for the surface integral, one has

$$\frac{\partial \rho_i}{\partial t} + \operatorname{div} j_i = R_i .$$

This equation is devoid of real contents until R and j are speci-fied. For this, explicitly biological hypotheses must be intro-duced. As regards R_i, to within the validity of the Volterra mech-anics, equations (1), we may, for example, place

$$R_i = \epsilon_i \rho_i + \frac{1}{\beta_i} \sum_j \alpha_{ji} \rho_j \rho_i , \qquad (9)$$

after recognizing that, properly speaking, the N's in (1) are really densities (spatially uniform in the case of (1)) rather than total population numbers.

Regarding j, the question is, What may be the nature of the motions of different organisms? We call to mind here the remark-able quantitative observations of Przibram (1913) on the motions of infusorians. Przibram's verification of the Einstein law—mean square displacement $\sim$ time—and his diagram of a paramecium track, so strikingly comparable to that of a Brownian particle, con-vince one that the motions of individuals are effectively *random walks;* whence the immediate conclusion that a host of the organ-isms will behave as does a host of molecules in solution: the motion on the whole will be a diffusion (Chandrasekhar, 1934), with a current den-sity proportional to the gradient of the population density, $j = -D\nabla\rho$. Here D stands for a diffusion constant characteristic of the partic-ular type of organism in a specified physical environment and has

the meaning, from the theory of random motion, $D = n\overline{r^2}/6$ (n = mean number of displacements/sec, $\overline{r^2}$ = expected squared displacement at any step). We are omitting, of course, consideration of any induced or systematic motion due, for instance, to mass motions of the medium containing the organisms.

To what extent is the random walk basically prevalent among other species, including higher animal species? It appears that in a qualitative way it may be so common as to be the rule rather than the exception. Witness Elton (1930):

"It puzzled at least one naturalist working in Siberia to find out how the squirrels all seemed to know where the richest food supply was to be found in any particular year, and how they managed to concentrate so successfully upon the good trees. The reason is simply that each individual is constantly going to and fro, reacting by migration to the conditions that it meets, and that these movements automatically result in a readjustment of the density of numbers in different places." It is interesting to compare this remark with one of Schrödinger's (1946) relative to molecular diffusion:

"That this random walk of the permanganate molecules, the same for all of them, should yet produce a regular flow ... is at first sight perplexing .... If you contemplate [in a schematic of a solution of varying concentration] thin slices of approximately constant concentration, the permanganate molecules which in a given moment are contained in a given slice, will, by their random walk, it is true, be carried with equal probability to the right or to the left. But precisely in consequence of this, a plane separating two neighboring slices will be crossed by more molecules coming from the left [higher concentration] than in the opposite direction, simply because to the left there are more molecules engaged in random walk than there are to the right."

One does not have to look far in even offhand observations of field life to receive the clear impression that the random walk or swim or flight, in a colloquial, if not a strictly technical, sense, is at bottom a dominant theme, though conditioned certainly by many factors. To the aerial observer, the squirrel in a homogeneous milieu may be reasonably expected to be like the paramecium to the inquiring microscopist.

We propose, then, the preliminary working hypothesis that self-diffusion owing to random-type motions of individuals is a basic

driving force for the phenomenon of migration; mathematically, that a principal connection between population currents and densities is

$$i_i = - D_i \nabla \rho_i. \tag{10}$$

While self-diffusion has been investigated to some extent, for example, by Skellam (1951), it covers only the case where the diffusional motions of different species are mutually non-interfering. Apart from the "point-interactions" between species described in equation (9), we must expect a motional type of interaction as well, that recognizes the possible bias, say, of the motion of predator toward prey and of prey away from predator. The currents and not only the densities must, in general, be coupled. Here one is reminded of the analogous situation in many-component diffusion theory (Kirkaldy, 1958), which gives us the suggestion that a suitable type of generalization of equation (10) is

$$i_i = - \sum_j D_{ij} \nabla \rho_j, \tag{11}$$

where generally the diffusion coefficients D_{ij} are ρ-dependent and may be explicitly time- and space-dependent as well. The contents of equation (11) must be understood, however, in quite a different sense from the physical one, where the coefficients D_{ij} are constrained by reciprocity laws of a very particular sort. For a prey species, 1, and a predator species, 2, for instance, one would write

$$i_1 = - D_1 \nabla \rho_1 - d_1 \nabla \rho_2,$$
$$i_2 = - D_2 \nabla \rho_2 + d_2 \nabla \rho_1, \tag{12}$$

or in terms of a diffusional-type drift velocity $\sim i$,
(net drift velocity of 1) = (self-diffusion velocity of 1) +
                                  (an escape velocity of 1 $\sim$ local gradient
                                                        of 2)

(net drift velocity of 2) = (self-diffusion velocity of 2) +

(a chase velocity of 2 ~ local gradient
of 1).

Thus a kind of diffusional race between the species in which, superposed on the self-diffusion of each species, are drifts experienced via the local gradients of the others—so to speak, each recognizing which way the population breeze of some of the others is blowing.

In this way is introduced an element counter to the purely homogenizing effect of simple diffusion, a necessary element in a satisfactory theory of migration.

The proposals above have some appearance of multicomponent hydrodynamics, quite mechanistic in character. Conspicuously absent is any reckoning of fluctuations of populations in a prescribed region. The strength of diffusion laws comes from the random motions of *immense numbers* of individuals; when the numbers are less than immense, the fluctuations of numbers, incomprehensible in a diffusion approximation supplying only more or less sharp averages, are of primary significance. One may perhaps regard the present suggestions as the tentative mechanical scheme that hides, or awaits, a thoroughly stochastic description of individual organism self-production, of organism encounters and interactions, and of organism motility.

We mention briefly some simple examples. For a single species under uniform physical conditions (bacteria or Protozoa in liquid culture) we have, by equations (8), (9), and (10),

$$\frac{\partial \rho}{\partial t} = D \nabla^2 \rho + \epsilon \rho .$$

The same equation governs the neutron density in a nuclear reactor (in the well-known diffusion approximation for the neutron motion); it will be seen, in fact, that reactor and culture are the same in essential aspects, with the exception of the boundary conditions: $\nabla \rho \cdot \hat{n} = 0$ at culture boundary, $\rho = 0$ (approximately) at reactor boundary. If, indeed, at the culture boundary there were escape or absorption of organisms (and $\epsilon > 0$), we should have a "critical ra-

dius," just as for a reactor, which, if exceeded, would give exponential growth and in the contrary case exponential decay.

By well-known methods, solutions to the differential equation suited to a given geometry and initial conditions may be constructed. Under spherical symmetry, for instance (florence flask seeded isotropically), one gets the superposition of diffusion modes,

$$\rho(r, t) = e^{\epsilon t} \left\{ C_0 + \sum_1^\infty C_n \, e^{-\frac{D x_n^2 t}{a^2}} \, \frac{\sin \left(x_n \frac{r}{a} \right)}{\left(\frac{r}{a} \right)} \right\},$$

where x_n are the roots 4.49, 7.85, ... , of $x_n = \tan x_n$, and a denotes flask radius, the C's being fixed by the initial distribution $\rho(r, 0)$. The first mode entirely controls the total population,

$$N_{\text{total}}(t) = \int_0^a 4\pi r^2 \, \rho(r, t) \, dr = C_0 \left(\frac{4}{3}\pi a^3 \right) e^{\epsilon t}.$$

Sighting along a thin diametral cylinder of length $2a$ and cross-section ΔS, as in a turbidity measurement, the enclosed population is

$$\Delta N = 2 \Delta S \int_0^a \rho(r, t) \, dr,$$

which can reveal something of what are the dominant modes and what is the value of the diffusion constant D.

A premonition of serious mathematical trouble is to be seen if the self-increase $\epsilon\rho$ is traded for the Verhulst $\epsilon\rho - \alpha\rho^2$,

$$\frac{\partial \rho}{\partial t} = D \nabla^2 \rho + \epsilon\rho - \alpha\rho^2.$$

The last term presents a difficulty that is only slightly ameliorated by the use of a linearization procedure allowing a discussion of just near-equilibrium.

As a second example, consider the extension of the Volterra periodic predator-prey relationship for two species, taking in equation (12) constant diffusion coefficients,

$$\frac{\partial \rho_1}{\partial t} - D_1 \nabla^2 \rho_1 - d_1 \nabla^2 \rho_2 = \epsilon_1 \rho_1 - \alpha_1 \rho_1 \rho_2 ,$$

$$\frac{\partial \rho_2}{\partial t} - D_2 \nabla^2 \rho_2 + d_2 \nabla^2 \rho_1 = - \epsilon_2 \rho_2 + \alpha_2 \rho_1 \rho_2 .$$

The non-linearity is awkward even in the cases of spatial homogeneity (all ∇^2 terms zero) or time stationarity (all $\partial/\partial t$ terms zero). Hence we limit ourselves for the present to small deviations from the temporal and spatial equilibrium state ($\rho_1 = \epsilon_2/\alpha_2$, $\rho_2 = \epsilon_1/\alpha_1$), writing $\rho_1 = \epsilon_2/\alpha_2 + Q_1$, $\rho_2 = \epsilon_1/\alpha_1 + Q_2$, and thence neglecting $Q_1 Q_2$,

$$\frac{\partial Q_1}{\partial t} - D_1 \nabla^2 Q_1 - d_1 \nabla^2 Q_2 + \lambda_1 Q_2 = 0 \qquad (\lambda_1 = \alpha_1 \epsilon_2/\alpha_2)$$

$$\frac{\partial Q_2}{\partial t} - D_2 \nabla^2 Q_2 + d_2 \nabla^2 Q_1 - \lambda_2 Q_1 = 0 \qquad (\lambda_2 = \alpha_2 \epsilon_1/\alpha_1).$$

Decoupling these, it is found that Q_1 or Q_2 satisfies

$$\frac{\partial^2 Q}{\partial t^2} - (D_1 + D_2) \nabla^2 \frac{\partial Q}{\partial t} + (D_1 D_2 + d_1 d_2) \nabla^4 Q - (\lambda_1 d_2 + \lambda_2 d_1) Q = 0,$$

wherein is seen a certain similarity to the wave equation or, more particularly, the equation of vibrations in elastic solids. The mixed term $\nabla^2 \partial Q/\partial t$, involving self-diffusion, in general will make for damping.

It is interesting to observe, in the case of negligible self-diffusion $(D_1, D_2 \simeq 0)$, when the sole driving forces for migration are chase and escape of predator and prey, that there are purely propagating plane-wave solutions, without dissipation,

$$Q = e^{i(k \cdot r - \omega t)}.$$

The frequency-wave-number spectrum follows the dispersion law,

$$\omega = \sqrt{d_1 d_2} \; \sqrt{k^2 + \frac{\lambda_1}{d_1}} \; \sqrt{k^2 + \frac{\lambda_2}{d_2}}.$$

As all wave numbers k are possible, a wave-packet of limited spatial extent may be Fourier-synthesized from wave numbers in the vicinity of some given one, k_0, and the packet will advance with the group velocity

$$\left(\frac{\partial \omega}{\partial k}\right)_{k_0} = \sqrt{d_1 d_2} \; k_0 \left(\sqrt{\frac{k_0^2 + \lambda_2/d_2}{k_0^2 + \lambda_1/d_1}} + \sqrt{\frac{k_0^2 + \lambda_1/d_1}{k_0^2 + \lambda_2/d_2}}\right).$$

We have a hint of how literally a group of organisms can move about as a unit.

Including, now, the self-diffusion, we find damped propagation, $\omega = \alpha - i\beta$,

$$\beta = \frac{1}{2}(D_1 + D_2) \, k^2$$

(hence strong damping of just the larger wave numbers), and

$$\alpha^2 = k^4 \left[d_1 d_2 - \left(\frac{D_1 - D_2}{2}\right)^2\right] + k^2 (\lambda_1 d_2 + \lambda_2 d_1) + \lambda_1 \lambda_2.$$

If, then, $D_1 = D_2$, the dispersion is as previously, and if $d_1 d_2 \geq (D_1 - D_2)^2/4$, every wave number is still possible; but if $d_1 d_2 < (D_1 - D_2)^2/4$, the coefficient of k^4 is negative, and only a finite range of wave numbers and frequencies is possible.

4. *Applications of the canonical ensemble.* We return now to the context of statistical-mechanical analysis of population based on the original Volterra scheme. The principal aim is to exhibit the power of the analysis in statistical questions relating to the time fluctuations of one species singled for study out of a great many. In using the canonical ensemble, we are assuming "thermodynamic" equilibrium, as previously described, in the large association encompassing the single species, that is, that the association has been let run a long time compared with any time of oscillation of any species. In particular, the use of a stationary ensemble is to signify that the single population-time curve is of the nature of a stationary time series, two long strips of the curve having the same statistical properties. As previously mentioned, the Gibbs averages are to be counted as time averages.

Let us notice first the earlier results, that, with G as in equation (6), $\overline{N_r} = q_r$, and that, from the canonical average of $(\partial G_r/\partial v_r)^2$ and of $v_r(\partial G_r/\partial v_r)$,

$$
\frac{\theta}{r_r} \equiv \frac{1}{x_r} = \frac{\overline{(N_r - \overline{N_r})^2}}{\overline{N_r}^2} = \left(\frac{N_r}{q_r} - 1\right) \log \frac{N_r}{q_r}, \tag{13}
$$

which gave the fundamental meaning of the association "temperature" θ as well as, in the last equality, a testable relationship. Thus x_r is to be construed as directly available observationally. The temperature itself, together with G, naturally is defined in the Gibbs distribution only to within a scale factor, as in ordinary physical thermometry; for its numerical determination any suitable reference state of equilibrium must first be assigned arbitrarily a numerical temperature θ_0, which, together with the totally stationary state, $\theta = 0$, of minimal entropy, establishes the size of the "degree" of temperature. This means that the parameter $r_r = \overline{N_r} \beta_r$ must also be of arbitrary scale, and so it is, upon recalling that the Volterra "equivalent numbers" β_r^{-1} have no individual significance but rather that only the composite $\beta_r^{-1}/\beta_s^{-1}$ has direct

meaning (number of s's lost or gained per number of r's gained or lost, per binary (r, s) encounter).

The quantity

$$D_r = \frac{\partial G_r}{\partial v_r} = r_r (e^{v_r} - 1) = r_r \left(\frac{N_r}{q_r} - 1\right)$$

is plainly of primary importance, so we record its moments (dropping the r):

$$\overline{D^n} = e^{\frac{\psi}{\theta}} \int_{-\infty}^{\infty} \left(\frac{\partial G}{\partial v}\right)^n e^{-\frac{G}{\theta}} \, dv$$

$$= e^{\frac{\psi}{\theta}} \left[\left(\frac{\partial G}{\partial v}\right)^{n-1} e^{-\frac{G}{\theta}} \Big|_{-\infty}^{+\infty} + \right.$$

$$\left. \theta(n-1) \int e^{-\frac{G}{\theta}} \left(\frac{\partial G}{\partial v}\right)^{n-2} \frac{\partial^2 G}{\partial v^2} \, dv \right]$$

or, since $\partial^2 G/\partial v^2 = \partial G/\partial v + r$,

$$\overline{D^n} = (n-1)\theta \, \overline{D^{n-1}} + (n-1)r\theta \, \overline{D^{n-2}},$$

$$\overline{D} = 0, \qquad \overline{D^2} = r\theta, \tag{14}$$

$$\overline{D^3} = 2r\theta^2, \quad \overline{D^4} = 6r\theta^3 + 3r^2\theta^2, \ldots.$$

The moments of $v = \log(N/q)$ may also be computed from the moment-generating function,

$$\overline{e^{\lambda v}} = \frac{\Gamma(\lambda + x)}{\Gamma(x)} x^{-\lambda},$$

so that

$$\overline{v} = \left(\frac{\partial}{\partial \lambda} \overline{e^{\lambda v}} \right)_{\lambda = 0} = \varphi(x) - \log x,$$

$$\overline{v^2} = \varphi'(x) + [\varphi(x) - \log x]^2, \ldots,$$

(15)

where φ denotes the digamma, φ' the trigamma function.

As a second step we consider averages involving derivatives of the v's. We have

$$\overline{\dot{v}_r} = e^{\frac{\psi}{\theta}} \sum_s \gamma_{sr} \int D_s \, e^{-\frac{G}{\theta}} \, dv_1 \ldots dv_n = 0,$$

since each $\overline{D}$ by (14) vanishes; also

$$\overline{\ddot{v}_r} = e^{\frac{\psi}{\theta}} \sum \gamma_{sr} \tau_s \int e^{v_s} \, \dot{v}_s \, e^{-\frac{G}{\theta}} \, dv_1 \ldots dv_n = 0,$$

since each $\dot{v}_s$ is independent of v_s and each $\overline{\dot{v}_s} = 0$. The combination $v_p \dot{v}_r$ must be expected to tell something of the interaction of species p and r,

$$\overline{v_p \dot{v}_r} = e^{\frac{\psi}{\theta}} \int v_p \left(\sum \gamma_{sr} \frac{\partial G_s}{\partial v_s} \right) e^{-\frac{G}{\theta}} \, dv_1 \ldots dv_n$$

$$= \gamma_{pr} \, \overline{v_p \frac{\partial G_p}{\partial v_p}} = \gamma_{pr} \, \theta.$$

Only the pth term in the $\sum_s$ survives, due to $\overline{D} = 0$. In similar

fashion,

$$\dot{v_r}\,\overline{\frac{\partial G_p}{\partial v_p}} = \dot{v_r}\,r_p\,\overline{(e^{v_p} - 1)} = \theta\,r_p\,\gamma_{pr}.$$

These give us the means of observing the "microscopic" parameters γ_{pr} of the Volterra theory,

$$\gamma_{pr} = \frac{1}{\theta}\,\overline{\frac{\dot{N_r}}{N_r}\,\log\frac{N_p}{q_p}} = \frac{1}{\theta}\,\overline{\frac{\dot{N_r}}{N_r}\left(\frac{N_p}{q_p} - 1\right)}\,, \qquad (16)$$

or, in terms of the original configuration of parameters entering the Volterra equations (1),

$$\overline{v_p\,\dot{v_r}} = \frac{\alpha_{pr}}{\beta_p\beta_r}\,\theta = \frac{\alpha_{pr}}{\beta_p}\,q_r\left(\frac{\theta}{r_r}\right)\,,$$

$$\frac{\alpha_{pr}}{\beta_p} = \overline{\frac{\dot{N_r}}{N_r}\,\log\frac{N_p}{q_p}}\,\bigg/\,\overline{q_r\left(\frac{N_r}{q_r} - 1\right)\log\frac{N_r}{q_r}}\,,$$

where the numerator may be replaced by the alternatives in (16) and the denominator by the alternative for θ/r in (13).

A basic meaning for the Volterra antisymmetry on the level of observable time averages now is

$$\overline{v_p\,\dot{v_r} + v_r\,\dot{v_p}} = \overline{\frac{d}{dt}\,v_p\,v_r} = 0.$$

Several other out of many interesting averages may be mentioned without proof:

$$\overline{\dot{v_p}\,\dot{v_r}} = \theta\,\sum\gamma_{ip}\,\gamma_{ir}\,r_i\,,$$

$$\overline{\dot{v}_r^{\,2}} = \theta \sum \gamma_{ir}^{\,2}\, r_i\,,$$

$$\overline{\ddot{v}_r\,(e^{v_r} - 1)} = -\,\theta \sum \gamma_{ir}^{\,2}\, r_i\,,$$

$$\overline{\ddot{v}_r\,(e^{v_r} - 1)^2} = -\,\frac{2\,\theta^2}{r_r} \sum \gamma_{ir}^{\,2}\, r_i\,,$$

$$\overline{\dot{v}_r \left(\frac{\partial G}{\partial v_p}\right)^n} = \gamma_{pr}\,\overline{D_p^{\,n}}\,,$$

$$\overline{\dot{v}_r^{\,2}\,(e^{v_p} - 1)} = 2\,\gamma_{pr}^{\,2}\,\theta^2\,.$$

We turn now to the basic problems of gauging something of the *horizontal* spreads of population-time curves.

The fraction T_-/T of a long time interval T spent by a population below the average population level $\overline{N}_r = q_r$ is the time average of

$$h(v_r) = 1,\ v_r < 0$$

$$= 0,\ v_r > 0.$$

Using the canonical ensemble, this is (dropping the subscript)

$$\frac{T_-}{T} = e^{\frac{\psi}{\theta}} \int_{-\infty}^{\infty} h(v)e^{-\frac{G}{\theta}}\,dv = \int_{-\infty}^{0} e^{-\frac{G}{\theta}}\,dv \Bigg/ \int_{-\infty}^{\infty} e^{-\frac{G}{\theta}}\,dv$$

$$= \int_{0}^{x} s^{x-1}\,e^{-s}\,ds \Bigg/ \int_{0}^{\infty} s^{x-1}\,e^{-s}\,ds,$$

after introducing $s = xe^v$ as variable of integration. In terms of Pearson's (1951) incomplete gamma-function,

$$I(u,p) \equiv \frac{1}{\Gamma(p+1)} \int_0^{u\sqrt{p+1}} e^{-s} s^p \, ds,$$

the mean below-average time is

$$\frac{T_-}{T} = I(\sqrt{x}, \, x - 1),$$

which varies between 0.5 and 1. It may be emphasized again that x is to be considered accessible to observation via equation (12). In Figure 1 is plotted T_-/T and its complement, the mean above-average time $T_+/T = 1 - T_-/T$. At very low association temperatures, $\theta < < r$, i.e., when the association is not far from the sta-
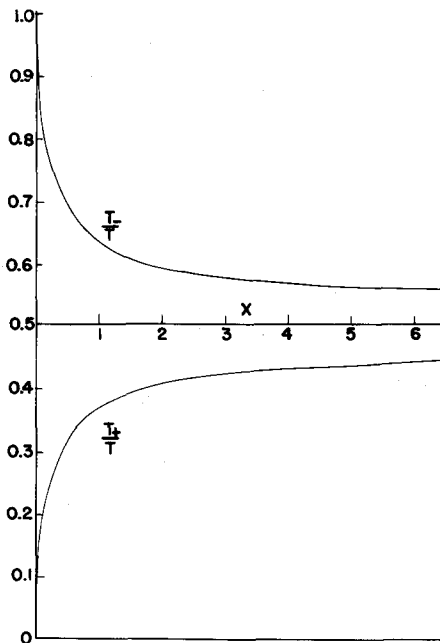
FIGURE 1. Mean below-average (T_-/T) and above-average (T_+/T) times as functions of x.

tionary state $N_r = q_r$ (all r), the populations spend as much time above as below their average levels, oscillating very roughly sinusoidally about these levels. For very high temperatures, far from the stationary state, the populations spend most of their time at below-average levels, oscillating below in long shallow troughs and above in short, high peaks.

To make more precise these views of the amplitudes of oscillation, we may append to the evaluation of T_+/T, T_-/T the calculation of the separate mean amplitudes A_+, A_- of oscillation below and above average, averaging separately over the time segments when $N > q$ and when $N < q$:

$$A_+ = \int_+ (e^v - 1)\, dt \bigg/ \int_+ dt = \int_+ \left(\frac{N}{q} - 1\right) dt \bigg/ \int_+ dt$$

$$= \frac{1}{T} \int_0^T (1 - h)(e^v - 1)\, dt \bigg/ \frac{T_+}{T}$$

$$= \frac{1}{\left(\dfrac{T_+}{T}\right)} e^{\frac{\psi}{\theta}} \int_0^\infty (e^v - 1)\, e^{-\frac{G}{\theta}}\, dv$$

$$= \frac{1}{\left(\dfrac{T_+}{T}\right)} \frac{x^x\, e^{-x}}{x!},$$

and similarly for A_- if (T_+/T) is replaced by (T_-/T). The $+$ on the integrals signifies times during which $N > q$. Figure 2 gives the amplitudes as functions of x, bearing out the approach to equality (and also over all decrease of amplitudes) for descending θ and the sharp increase of A_+ over A_- for ascending θ.

A key datum of great practical interest to be comprehended within a demographic theory is the frequency of oscillation of a
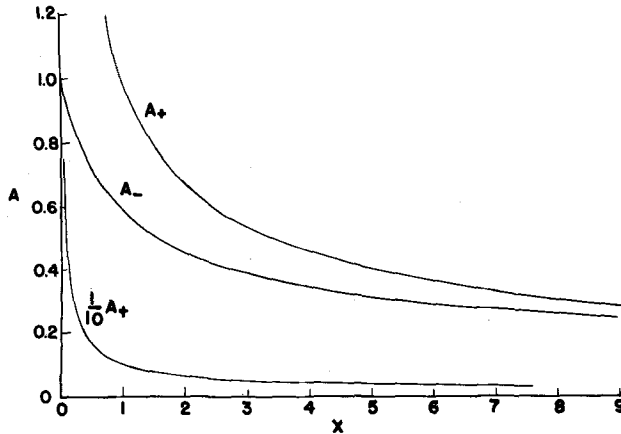
FIGURE 2. Mean amplitudes of oscillation above (A_+) and below (A_-) average.

population. It is surprisingly difficult to bring forth this informa-tion explicitly, even in the simple case of the periodic two-species Volterra interaction, but it turns out to be fairly amenable to treat-ment by the canonical ensemble.

Consider an oscillatory function $F(t)$. The integral

$$\int_0^T \delta\left(F(t)\right) dt,$$

where δ designates the delta-function, will give a contribution

$$\int \delta\left(F'(t_0)\,(t - t_0)\right) dt = \frac{1}{\left| F'(t_0) \right|}$$

near a zero $t = t_0$ of F, but not otherwise. Therefore, the mean frequency of zeroes, ω, of $F(t)$ is*

$$\omega = \frac{1}{T} \int_0^T \left| F'(t) \right| \, \delta\left(F(t)\right) dt.$$

*I am indebted to Professor M. Kac for pointing out to me this result and its utility in the statistical mechanics.

For the mean frequency of zeroes of a population about the level $N_r = q_r$ or equivalently about $v_r \equiv \log N_r/q_r = 0$, we then have, using a Gibbs average for the time average,

$$\omega_r = e^{\frac{\psi}{\theta}} \int |\dot{v}_r| \; \delta(v_r) \; e^{-\frac{G}{\theta}} \; dv_1 \ldots dv_n.$$

Since $\dot{v}_r$ is independent of v_r, this breaks up into a simple integral over v_r and a more difficult one over the rest of phase space dv',

$$\omega_r = e^{\frac{\psi_r}{\theta}} e^{-\frac{G_r(0)}{\theta}} \int |\dot{v}_r| \; e^{-\frac{G-G_r}{\theta}} dv'$$

$$= e^{\frac{\psi_r}{\theta}} e^{-x_r} \overline{|\dot{v}_r|} = \frac{x_r^{x_r} e^{-x_r}}{\Gamma(x_r)} \overline{|\dot{v}_r|}; \tag{17}$$

so the computation reduces to that of $\overline{|\dot{v}_r|}$.

By a slight extension of the foregoing we also find the mean frequency of zeroes of N/q about an arbitrary line $N/q = \nu$ to be

$$\omega_r\left(\frac{N}{q} - \nu\right) = e^{\frac{\psi}{\theta}} \int e^{-\frac{G}{\theta}} |\dot{v}_r \; e^{v_r}| \; \delta(e^{v_r} - \nu) \; dv_1 \ldots dv_n$$

$$= e^{\frac{\psi_r}{\theta}} e^{-x_r \nu} \nu^{x_r} \overline{|\dot{v}_r|}.$$

Comparing with the previous result for $\omega_r\left(\frac{N}{q} - 1\right)$, we have

$$\omega_{\text{rel}}(\nu) = \frac{\omega_r\left(\frac{N}{q} - \nu\right)}{\omega_r\left(\frac{N}{q} - 1\right)} = e^{x_r} (\nu e^{-\nu})^{x_r}$$

$=$ frequency about $\dfrac{N}{q} = \nu$ relative to frequency about $\dfrac{N}{q} = 1$.

Since $\omega_{\text{rel}}(\nu) < 1$ if $\nu > 1$ or $\nu < 1$, we find that N/q crosses the axis $N/q = 1$ more frequently than any other axis $N/q = \nu$. How

much less is the frequency of oscillation about axes other than $N = q$ is to be seen in Figure 3, where contours of $\omega_{rel} = const$ in the x, ν plane are shown. It is evident that the frequency of zeroes falls off with extreme rapidity about increasingly elevated axes for the lower association temperatures (higher x) and that only if $\theta >> \tau$ is the fall-off slow. This is to say, looking also at $\nu < 1$, that at low temperatures small excursions away from $N = q$ occur appreciably more frequently than larger ones (with more small upward excursions than downward), and contrariwise for high temperatures.

The variable $v = \log N/q$ is of as much interest as N, and for its zeroes-frequency about $v = \nu$ (ν now any positive or negative value) is found

$$\omega_r(v - \nu) = \frac{x^x}{\Gamma(x)} e^{-x(e^\nu - \nu)} \overline{|\dot{v}_r|} .$$

The rigorous computation of $\overline{|\dot{v}_r|}$ unfortunately seems to be out of the question, though satisfactory approximations are to be had.
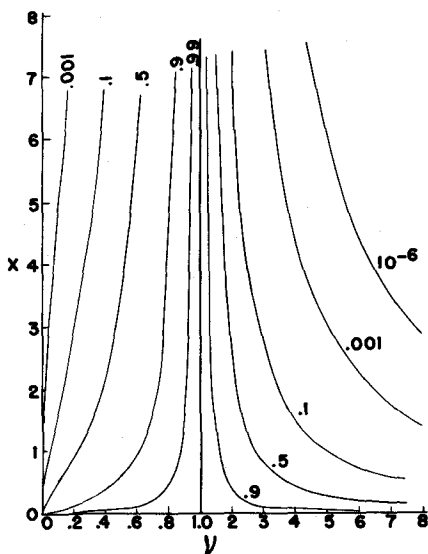

FIGURE 3. Contours of $\omega_{rel} = const$ in the x, ν plane.

The magnitude of the difficulty may be seen by writing

$$|\dot{v}_r| = \frac{1}{\pi} \int_{-\infty}^{\infty} \frac{1 - \cos \dot{v}_r \xi}{\xi^2} \, d\xi$$

and then

$$\overline{|\dot{v}_r|} = \frac{e^{\psi'/\theta}}{\pi} \int_{-\infty}^{\infty} \frac{d\xi}{\xi^2} \int e^{-G'/\theta} (1 - \cos \dot{v}_r \, \xi) \, dv',$$

primes denoting the absence of the variable v_r. Performing the integration over phase space, after placing $\dot{v}_r = \Sigma \, \gamma_{ir} \, r_i (e^{v_i} - 1)$, gives

$$\overline{|\dot{v}_r|} = \frac{1}{\pi} \int_{-\infty}^{\infty} \frac{d\xi}{\xi^2} [1 - \text{Re} \; \Omega(\xi)],$$

where

$$\Omega = \prod_{i \neq r} \frac{e^{-i\xi \, \tau_i \gamma_{ir}}}{(1 - i \, \xi \, \theta \gamma_{ir})^{x_i}} = e^{i \, \xi \, \epsilon_r} \prod_{i \neq r} (1 - i \, \xi \, \theta \gamma_{ir})^{-x_i}$$

is the characteristic function of $\dot{v}_r$, and by equation (2), $\Sigma \, r_i \gamma_{ir} = - \epsilon_r$. Plainly, $\dot{v}_r$ has a complicated distribution, and to find $\overline{|\dot{v}_r|}$ is to seek the Fourier transform of a difficultly transformable function. From Ω are visible the semi-invariants of $\dot{v}_r$,

$$\kappa_1 = 0, \quad \kappa_2 = 1! \; \theta \, \overline{\gamma^2}, \quad \kappa_3 = 2! \; \theta \, \overline{\gamma^3},$$

where $\overline{\gamma^2} = \Sigma \, r_i \gamma_{ir}^2$, $\overline{\gamma^3} = \Sigma \, r_i \gamma_{ir}^3$, ..., etc., so that the moments

of $\dot{v}_r$ come to be

$$\overline{\dot{v}_r} = 0, \quad \overline{\dot{v}_r{}^2} = \theta\,\overline{\gamma^2},$$

$$\overline{\dot{v}_r{}^3} = 2\,\theta^2\,\overline{\gamma^3}, \quad \overline{\dot{v}_r{}^4} = 3\,\theta^2\,\overline{\gamma^2}^{\,2} + 6\,\theta^3\,\overline{\gamma^4},$$

$$\overline{\dot{v}_r{}^5} = 20\,\theta^3\,\overline{\gamma^2}\,\overline{\gamma^3} + 24\,\theta^4\,\overline{\gamma^5}, \dots,$$

from which may be determined approximate distribution functions of Gram-Charlier or Pearson type. The appearance of the moments $\overline{\gamma^2}, \overline{\gamma^3}, \dots$, raises the interesting side question whether there may not be another order of statistics connected with the considerable ignorance surrounding the numerous microscopic parameters; whether, so to speak, equation 2, $(\epsilon) = \gamma(r)$, does not define in some way a kind of algebraic statistics on all vectors (ϵ) and transformations γ, admitting only positive vectors (r), over which canonical averages would be further averaged.

For sufficiently small θ we have

$$\Omega = \exp - \Sigma\,[i\,\xi\,r_i\,\gamma_{ir} + x_i\,\log\,(1 - i\,\xi\,\theta\,\gamma_{ir})]$$

$$\simeq \exp - \Sigma\,i\,\xi\,r_i\,\gamma_{ir} + x_i\,[-i\,\xi\,\theta\,\gamma_{ir} - \frac{1}{2}\,(i\,\xi\,\theta\,\gamma_{ir})^2]$$

$$\simeq \exp - \frac{1}{2}\,\xi^2\,\theta\,\overline{\gamma^2},$$

and for $\overline{|\dot{v}_r|}$

$$\overline{|\dot{v}_r|} = \left(\frac{2}{\pi}\right)^{\frac{1}{2}} (\theta\overline{\gamma^2})^{\frac{1}{2}} = \left(\frac{2}{\pi}\right)^{\frac{1}{2}} (\overline{\dot{v}_r{}^2})^{\frac{1}{2}}. \tag{18}$$

We are using here effectively the fact that at sufficiently small θ the distribution of $n_i = e^{v_i}$,

$$P(n_i)\,dn_i = \frac{x_i{}^{x_i}}{\Gamma(x_i)}\,e^{-x_i n_i}\,n_i{}^{x_i - 1}$$

is sensibly normal, so that

$$\dot{v}_r = \Sigma \; \gamma_{ir} \; \tau_i \; (n_i - 1) = \Sigma \; \gamma_{ir} \; \tau_i n_i + \epsilon_r$$

is also essentially normally distributed.

One has the suggestion here to appeal to the central limit theorem and to say that, in general, $\dot{v}_r$, being a superposition of a great many independent variates, tends to be normally distributed without restriction on θ. This may in fact be made quite plausible (if not conclusive) in spite of the awkward characteristics of $P(n)$ for larger θ. Adopting this suggestion, equation (18) holds generally, giving, for the zeroes-frequency of v_r,

$$\omega_r = \left(\frac{2}{\pi}\right)^{\frac{1}{2}} (\tau_r \, \overline{\gamma^2})^{\frac{1}{2}} \; \frac{x^{x + \frac{1}{2}} e^{-x}}{x!}. \tag{19}$$

Hence ω_r is slowly and monotonically varying with x (Fig. 4). While at $\theta = 0$ (where the association is completely quiet, all $N_r(t) = q_r$) the oscillation frequency is zero, as soon as the association is the least bit excited, the frequency jumps to its largest value, decreasing thereafter uniformly as θ is raised. The discontinuity in ω at zero temperature is, of course, to be expected
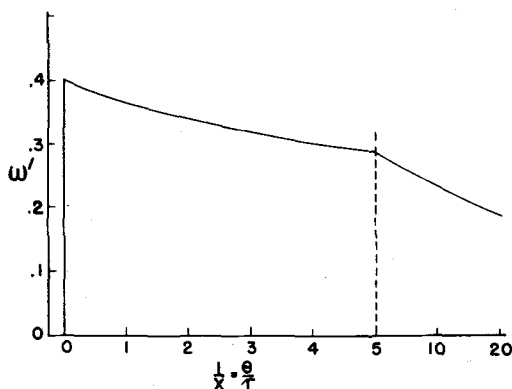

FIGURE 4. Mean frequency of oscillation ω about $N = q$. Ordinate ω' is ω of equation (19) with the constant factors omitted.

insofar as the perturbation of an initially quiet oscillatory system must result at once in a finite frequency, if only an infinitesimal amplitude.

It may be that, hiding behind the smoothness of (19) and covered over by the use of the central limit theorem, there is some more or less fine structure, a slight waviness, in the variation of ω with θ.

It is interesting to compare the frequency of oscillation found above with that which would occur if $v(t)$ were random (Gaussian) noise. To this end we first generalize (19) to give the frequency of oscillation of v about its average, $\overline{v}$ (eq. (15)),

$$\omega_r(v_r - \overline{v_r}) = \overline{\delta(v_r - \overline{v_r}) \, |\dot{v}_r|} = \overline{\delta(v_r - \overline{v_r})} \; \overline{|\dot{v}_r|}$$

$$= \left(\frac{2}{\pi}\right)^{\frac{1}{2}} (\overline{r\gamma^2})^{\frac{1}{2}} \frac{x^{x+\frac{1}{2}}}{x!} \exp - x \, [e^{\varphi - \log x} - (\varphi - \log x)].$$

Now, if $U(t) = v - \overline{v}$ were a random noise, the mean frequency of zeroes would be (Rice, 1944)

$$f = \frac{1}{\pi} (- \overline{U \ddot{U}} / \overline{U^2})^{\frac{1}{2}}.$$

Using canonical averages,

$$\overline{U \ddot{U}} = \overline{(v - \overline{v}) \ddot{v}} = \overline{v \ddot{v}} = - \theta \gamma^2,$$

$$\overline{U^2} = \overline{(v - \overline{v})^2} = \overline{v^2} - \overline{v}^2 = \varphi'(x);$$

whereupon

$$f = (\overline{r\gamma^2})^{\frac{1}{2}} \frac{1}{\pi} [x \, \varphi'(x)]^{-\frac{1}{2}}.$$

In Figure 5 are plotted f and $\omega(v - \overline{v})$, omitting the common factor $(\overline{r\gamma^2})^{\frac{1}{2}}$. The two results are altogether comparable; the intima-
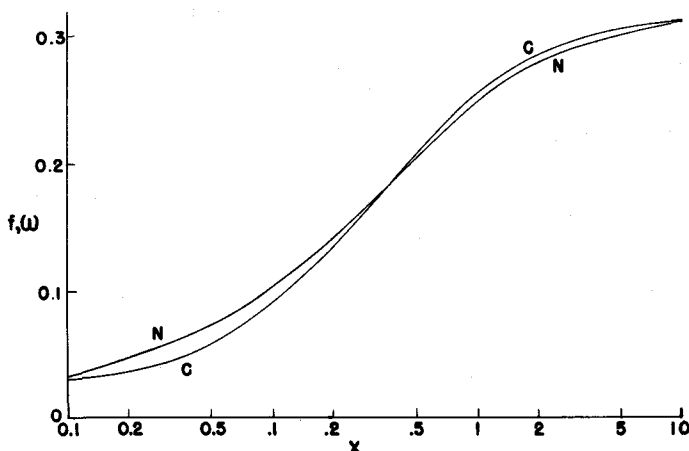
FIGURE 5. Mean frequency of oscillation of v about $v = \bar{v}$ (curve $C\text{-}C$) compared to similar result if v were random noise (curve $N\text{-}N$); factor $(\overline{r\gamma^2})^{\frac{1}{2}}$ has been dropped in both curves.

tion is that $U(t)$ is possibly not far different from random noise in a general way.

In passing, it may be mentioned that one may make over the population fluctuations into something very apt to be like random noise by introducing, instead of v, the function $Q(v)$, defined by

$$\frac{x^x}{\Gamma(x)} e^{-x(e^v - v)} \, dv = \frac{1}{a\sqrt{2\pi}} e^{-\frac{1}{2}\frac{Q^2}{a^2}} \, dQ, \qquad (20)$$

that is, by making over the v-distribution into a normal one; this is only necessary and not sufficient for $Q(t)$ to be a random noise. For large $x\,(\theta < < r)$ the v-distribution is already normal,

$$\frac{x^x}{\Gamma(x)} e^{-x(e^v - v)} \simeq \frac{x^x e^{-x}}{\Gamma(x)} e^{-\frac{1}{2}xv^2} \simeq \left(\frac{x}{2\pi}\right)^{\frac{1}{2}} e^{-\frac{1}{2}xv^2}$$

(using the Stirling approximation in the last step), so we are guided to $a = x^{-\frac{1}{2}}$. Integrating (20) on the left from 0 to v, and on the right

from Q_0 to Q, $Q(v)$ is then completely defined by

$$I(\sqrt{x}\, e^v, \, x-1) - I(\sqrt{x}, \, x-1) = E\left(Q\ \sqrt{\frac{x}{2}}\right) - E\left(Q_0\ \sqrt{\frac{x}{2}}\right),$$

E denoting the error function,

$$E(z) = \frac{1}{\sqrt{\pi}} \int_0^z e^{-t^2}\, dt.$$

The constant Q_0 is chosen so that Q ranges from $(-\infty, \infty)$ when v does, or

$$E\left(Q_0\ \sqrt{\frac{x}{2}}\right) = I(\sqrt{x}, \, x-1) - \frac{1}{2}.$$

5. *Comparison with observation.* If we settle for a treatment *grosso modo* for ecological field data, some test of a number of theoretical conclusions is possible. For the meaningful evaluation of time-averages, population data extending over a sufficiently long time are needed. One of the longest unbroken records, Figure 6, seems to be the catch of foxes by the Moravian missions in Labrador from 1834 to 1925. Elton (1942) has compiled (chap. 13, Table 17) and discussed the data. We shall assume simply that the fox-catch accurately samples the population, an assumption that is not unreasonable, judging from Elton's elaborate discussion (chaps. 14 and 15). The catches represent intra-annual averages and so, desirably for our purposes, they average over seasonal and other smaller-scale fluctuations outside the present theoretical framework. Rather than attempt to smooth the data, which would be at best somewhat ambiguous and could unduly bias the computation of time-averages, we leave them entirely un-processed, taking the polygonal line in the upper part of Figure 6 as the population-time curve.
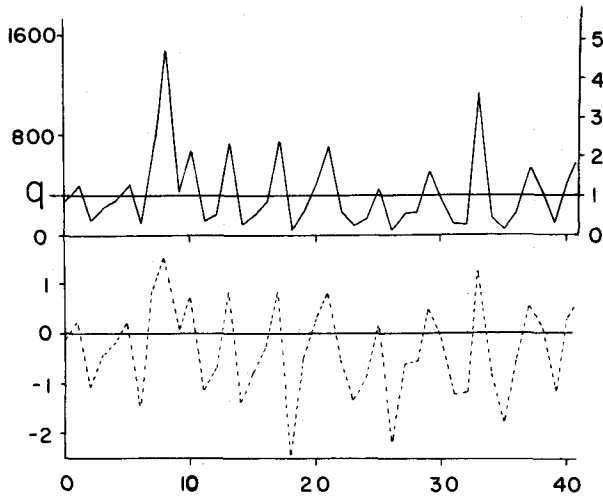
FIGURE 6. Labrador fox-catches for the first 40 years of a 91-year period, after Elton (1942).   Upper curve gives the catch directly (left-hand scale); right-hand scale gives the reduced variable $n = N/q$. Lower curve shows $v(t)$.

In Table 1 we record the directly computed time-averages of several quantities, the theoretically consequent values of x, and the excursions in the latter due to a ± 10 per cent alteration of the former.

Aside from the assumption that catch $\sim$ population, errors in the reduction of the data are: statistical errors due to the rather small time interval of 91 years covering the data; and the errors of the assumed polygonal shape of the population curve. Over all, an error of 10 per cent in any time average would seem to be a modest estimate.   The uniformity of x-values, which is the test of the theory, is in this light even a little surprising.

TABLE 1

	Time Average	x	Excursion
T_-/T	0.595	1.90	0.70–15.0
A_-	.445	2.10	1.00–2.75
A_+	.729	1.71	1.42–2.05
$(n-1)^2$	.536	1.87	1.69–2.07
$(n-1)\log n$	.489	2.04	1.86–2.27
$\log n$	-0.258	2.08	2.31–1.91

In Figure 7 is shown $\omega_{rel}(\nu)$ observationally and theoretically. Here the statistical errors are very appreciable, on the order of perhaps 50 per cent, since each datum involves the ratio of the count of zeroes on two axes, each count having itself a large error (maximum count = 43, on axis $n = 1$). The shape of $\omega_{rel}(\nu)$ must be considered to be satisfactorily accounted for.

The testing of absolute and not relative zeroes-frequencies would be desirable but, as this involves a reckoning of a time derivative ($\dot{v}$), is scarcely feasible under the "polygonal" assumption. However, even with this assumption, it is found that $\overline{|\dot{v}|} = 1.152 \ yr^{-1}$, $\omega(n-1) = 43/91 \ yr^{-1}$, giving, according to equation (17), $x = 1.25$, and an excursion induced by a 20 per cent error in $\omega/|\dot{v}|$ of $1.70 - 0.84$. The polygonal assumption, of course, greatly falsifies $\overline{|\dot{v}|}$, giving an overestimate; any reasonable smoothing decreases $\overline{|\dot{v}|}$ noticeably. For example, assuming that $\dot{v}$ varies linearly over one-year intervals $t, t+1$ between the limits $\left[v\left(t + \frac{1}{2} \right) - v\left(t - \frac{1}{2} \right) \right]$ and $\left[v\left(t + \frac{3}{2} \right) - v\left(t + \frac{1}{2} \right) \right]$, where these v's are taken right from the data, one gets $\overline{|\dot{v}|} = 0.841 \ yr^{-1}$, giving $x = 2.16$.

The comparison of theory and observation outlined here is, on the whole, more a test of the probability law 7 than of the under-
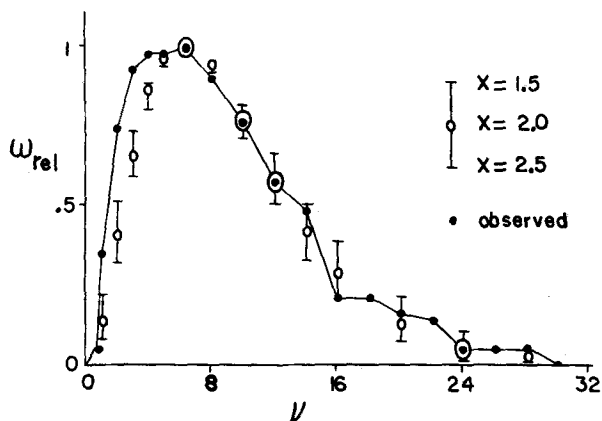

FIGURE 7. Comparison of theoretical and observed $\omega_{rel}(\nu)$. Abscissa is ν in units of 0.16, which correspond to intervals of 50 fox-catches in Figure 1.

lying Volterra mechanics; a significant exception is the testing of ω_{rel} and ω, which relies on the basic property of the mechanics, that $\dot{v}_i$ is independent of v_i.

One test does not, in general, make (or unmake) a theory; but we have at least the intimation of validity of the Volterra statistical mechanics. It is difficult to escape an impression in the present case that a Volterra oscillation is effectively, if not literally, at hand and that the statistical theory can be a useful tool in the interpretation and correlation of ecological field data. Further tests would be highly desirable: particularly, for instance, the testing of $d/dt(v_i v_j) = 0$ for two strongly interacting species, that hinges so evidently on the basic premise of antisymmetry of γ_{ij}.

6. *Non-stationary ensembles.* There is one case in which thermodynamically non-equilibrium configurations of macroscopic systems can at present be profitably treated within the Gibbs methodology, that of a sufficiently slow alteration of external variables or of the system temperature. We shall adapt the discussion of Cox (1950) to a sketch of this case for the macroscopic Volterra systems.

Representative types of external variables of importance in biological associations are the physical temperature or radiation intensity or oxygen tension in the environment, and the question to be answered is, What Gibbs ensemble is appropriate for the description of the association when such variables vary and induce changes in the microscopic parameters ϵ, β, α (eq. (1))? Additionally, the association temperature θ may be subject to change through contacts with a second association at different temperature.

A slight revision of the "canonical" demographic equations (3) is first called for so as to make the meaning of phase space independent of changes of the external variables, X. Let ϵ, β, α be $\epsilon(X)$, $\beta(X)$, $\alpha(X)$, with $X = X(t)$, and let X_0 be some fixed reference values of the X. Calling $q_s = q_s(X)$ and $q_{s0} = q_s(X_0)$ the solutions to equations (2) for the indicated values of X, and redefining the v's as $v_r \equiv \log(N_r/q_{r0})$, the Volterra equations become

$$\dot{v}_r = \sum_s \gamma_{sr}\,(\beta_s\,q_{s0}\,e^{v_s} - \beta_s\,q_s) = \sum_s \gamma_{sr}\,\frac{\partial G}{\partial v_s},$$

where $\gamma = \gamma(X)$ and G, no longer a constant of the motion, is

$$G = \Sigma \; (\beta_r \; q_{r0} \; e^{v_r} - \beta_r \; q_r \; v_r).$$

Imagine, now, that one or more of the X_i, or θ, changes so slowly that a glance at the association shows it to be nearly in thermodynamic equilibrium with the momentarily prevailing $G(X)$, giving, in the canonical distribution, a close approximation to the true density-in-phase. "Momentarily" means a sufficiently long moment for a good time-average of some population variable to be taken, but so short on the time-scale of the changes in X or θ that $G(X)$ varies only slightly in most parts of phase space. In short, the changes envisioned are quasi-static, the system being gently propelled through a succession of near-equilibrium states; it is only in this case that it makes sense still to speak of a system-temperature at all. In seemingly sharp contrast to the physical case, the "moment" biologically must be on the order of months or years, and the secular changes measured as increments per decade or century.

Following Cox, we suppose that the corrections to the instantaneous canonical distribution are proportional to the adequately small velocities of change of the drifting X and θ,

$$\rho = e^{\frac{\psi - G}{\theta}} \; (1 + A \; \dot\theta + B_1 \; \dot X_1 + B_2 \; \dot X_2 + \ldots)$$

$$= \rho_0 \; (1 + A \; \dot\theta + B_1 \; \dot X_1 + B_2 \; \dot X_2 + \ldots). \qquad (21)$$

The A, B are taken to be functions of θ, X, v, but not of $\dot\theta$, $\dot X$. They are fixed by Liouville's equation,

$$\frac{\partial \rho}{\partial t} = - \sum \dot v_r \; \frac{\partial \rho}{\partial v_r},$$

which now reads, after dropping a factor ρ_0 throughout,

$$\left(\sum_i \frac{1}{\theta} \left(\frac{\partial \psi}{\partial X_i} - \frac{\partial G}{\partial X_i} \right) \dot X_i - \frac{\psi - G}{\theta^2} \; \dot\theta \right) (1 + A \; \dot\theta + B_1 \; \dot X_1 + \ldots) +$$

$$A\ddot{\theta} + B_1 \ddot{X}_1 + \ldots = -\sum_r \dot{v}_r \left(-\frac{1}{\theta}\frac{\partial G}{\partial v_r}\right)(1 + A\dot{\theta} + B_1 \dot{X}_1 + \ldots) -$$

$$\sum_r \dot{v}_r \left(\frac{\partial A}{\partial v_r}\dot{\theta} + \frac{\partial B_1}{\partial v_r}\dot{X}_1 + \ldots\right).$$

On the left, products and derivatives of $\dot{\theta}$, $\dot{X}$ may be dropped; on the right, the first term vanishes, owing to $\Sigma \dot{v}_r \partial G/\partial v_r = 0$. In what remains we may equate coefficients of the small but arbitrary $\dot{\theta}$, $\dot{X}_i$, giving

$$\frac{\psi - G}{\theta^2} = \sum_r \dot{v}_r \frac{\partial A}{\partial v_r},$$

$$\frac{1}{\theta}\left(\frac{\partial \psi}{\partial X_i} - \frac{\partial G}{\partial X_i}\right) = -\sum_r \dot{v}_r \frac{\partial B_i}{\partial v_r}. \tag{22}$$

These are partial differential equations for A, B. Since in equation (21) both ρ and ρ_0 represent normalized probability densities, A and B_i have the restriction $\overline{A} = 0$, $\overline{B}_i = 0$, where the bar designates an average over the unperturbed density ρ_0.

We note a characteristic *lack* of reciprocity of the Onsager type. Define, for convenience,

$$\frac{\delta B}{\delta t} \equiv \frac{dB}{dt} - \frac{\partial B}{\partial t} = \sum_r \frac{\partial B}{\partial v_r}\dot{v}_r,$$

and take the ρ-average of (22), denoted by the double bar,

$$\overline{\overline{F}}_1 \equiv -\overline{\overline{\frac{\partial G}{\partial X_1}}} = \text{average "force" conjugate to } X_1$$

$$= -\frac{\partial \psi}{\partial X_1} - \theta \left(\overline{\frac{\delta B_1}{\delta t}} + \dot{\theta} A \overline{\frac{\delta B_1}{\delta t}} + \dot{X}_1 B_1 \overline{\frac{\delta B_1}{\delta t}} + \dot{X}_2 B_2 \overline{\frac{\delta B_1}{\delta t}} + \dots \right),$$

$$\overline{\overline{F}}_2 = -\frac{\partial \psi}{\partial X_2} - \theta \left(\overline{\frac{\delta B_2}{\delta t}} + \dot{\theta} A \overline{\frac{\delta B_2}{\delta t}} + \dot{X}_1 B_1 \overline{\frac{\delta B_2}{\delta t}} + \dots \right).$$

Also

$$\overline{\overline{S}} = -\overline{\overline{\log \rho}} = \text{system entropy}$$

$$= -\frac{\overline{\psi - G}}{\theta} - \theta \left(\dot{\theta} A \overline{\frac{\delta A}{\delta t}} + \dot{X}_1 B_1 \overline{\frac{\delta A}{\delta t}} + \dot{X}_2 B_2 \overline{\frac{\delta A}{\delta t}} + \dots \right).$$

We now find the further restrictions on B_i, $\overline{\delta B_i / \delta t} = 0$, and

$$\frac{\partial \overline{\overline{F}}_1}{\partial \dot{\theta}} = -\theta A \overline{\frac{\delta B_1}{\delta t}} \neq \frac{\partial \overline{\overline{S}}}{\partial \dot{X}_1} = -\theta B_1 \overline{\frac{\delta A}{\delta t}},$$

$$\frac{\partial \overline{\overline{F}}_1}{\partial \dot{X}_2} = -\theta B_2 \overline{\frac{\delta B_1}{\delta t}} \neq \frac{\partial \overline{\overline{F}}_2}{\partial \dot{X}_1} = -\theta B_1 \overline{\frac{\delta B_2}{\delta t}},$$

whereas for physical systems the inequality is an equality.

The differential equations (22) have been solved in some restricted cases, but the further elaboration of non-equilibrium awaits their more general analysis.

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