

On Coupled Rate Equations with Quadratic Nonlinearities (population growth and competition)

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ABSTRACT Rate equations with quadratic nonlinearities appear in many fields, such as chemical kinetics, population dynamics, transport theory, hydrodynamics, etc. Such equations, which may arise from basic principles or which may be phenomenological, are generally solved by linearization and application of perturbation theory. Here, a somewhat different strategy is emphasized. Alternative nonlinear models that can be solved exactly and whose solutions have the qualitative character expected from the original equations are first searched for. Then, the original equations are treated as perturbations of those of the solvable model. Hence, the function of the perturbation theory is to improve numerical accuracy of solutions, rather than to furnish the basic qualitative behavior of the solutions of the equations.

Introduction and population growth equations

Many phenomena—physical, biological, and social—are modeled by differential equations with quadratic nonlinearities. A standard way of dealing with these is to linearize them, solve the linearized equation, and occasionally treat the nonlinear terms as perturbations. Often, high-order perturbation theory is necessary to yield the special qualitative features of the problem that are due to the nonlinearity. The object of this paper is to describe a perturbation method in which one starts with a related solvable nonlinear model, and treats the problem of interest as the perturbed version of the nonlinear one. To motivate our scheme, I start with an examination of two elementary population growth and competition models, then generalize the ideas used to treat more complicated systems.

We first examine the Verhulst equations for population growth (1)

$$\dot{n} \equiv dn/dt = kn(\theta - n)/\theta. \quad [1]$$

The population saturates at θ , and has the logistic time development

$$n(t) = \theta n(0) / \{n(0) + [\theta - n(0)] \exp(-kt)\} \quad [2]$$

which has the required saturation shape as given in Fig. 1. An alternative to [1] is the Gompertz (2) equation, linear in $\log(n/\theta)$,

$$\dot{n} = -kn \log(n/\theta) \text{ or } [\log(n/\theta)]_t = -k \log(n/\theta) \quad [3]$$

so that

$$n(t) = \theta \exp\{e^{-kt} \log[n(0)/\theta]\} \quad [4]$$

In Fig. 1, the curves that represent [2] and [4] are similar, the basic difference being that [2] is symmetrical around the inflection point, while [4] is not.

The next more complicated example to be considered comes from the Lotka-Volterra prey-predator equations (3-5)

$$\dot{n}_1 = k_1 n_1 - \lambda_1 n_1 n_2, \quad \dot{n}_2 = -k_2 n_2 + \lambda_2 n_2 n_1 \quad [5]$$

where n_1 represents the population of the prey that would grow exponentially in absence of predator, ($n_2 = 0$). Note that n_2 would decay exponentially without prey. At equilibrium, $n_2 = q_2 \equiv k_1/\lambda_1$ and $n_1 = q_1 \equiv k_2/\lambda_2$. If initially n_1 and n_2 deviate from equilibrium, we define δ_i by $n_i = q_i(1 + \delta_i)$, so that to first order in the δ_i :

$$\dot{\delta}_1 = -k_1 \delta_2 \text{ and } \dot{\delta}_2 = k_2 \delta_1 \text{ or } \ddot{\delta}_1 = -k_1 k_2 \delta_1 \quad [6]$$

The solution of these linear equations is

$$\delta_1(t) = \{ [k_2 \delta_1^2(0) + k_1 \delta_2^2(0)] / k_2 \}^{1/2} \cos(\omega t + \eta) \quad [7]$$

$$\delta_2(t) = \{ [k_2 \delta_1^2(0) + k_1 \delta_2^2(0)] / k_1 \}^{1/2} \sin(\omega t + \eta) \quad [8]$$

$$\omega = (k_1 k_2)^{1/2} \text{ and } \tan \eta = (k_1/k_2)^{1/2} \{ \delta_1(0) / \delta_2(0) \} \quad [9]$$

Notice that for all initial conditions, the time variation of $\delta_1(t)$ and $\delta_2(t)$ is sinusoidal. There seems to be no simple analytical solution of the full nonlinear Lotka-Volterra equations [7], but numerical solutions as plotted in Fig. 2 exhibit a spiking tendency, which becomes stronger as the initial conditions recede from the steady state. This spiking effect reflects the nonlinear character of the basic rate equations.

Taking a cue from Gompertz's model (6), we can obtain the spiking effect from a nonlinear model, which can be solved by making a logarithmic transformation of the dependent variables. Notice that the Lotka-Volterra equations can be written (with $k_i' = k_i - \lambda_i$),

$$\dot{n}_1/n_1 = k_1' - \lambda_1(n_2 - 1); \quad \dot{n}_2/n_2 = -k_2' + \lambda_2(n_1 - 1) \quad [10]$$

These equations are a special case with $\alpha = 1$ of the set

$$\begin{aligned} \dot{n}_1/n_1 &= k_1' - (n_2^\alpha - 1)/\alpha; \\ \dot{n}_2/n_2 &= -k_2' n_2 + \lambda_2 n_2 (n_1^\alpha - 1)/\alpha \end{aligned} \quad [11]$$

If $\{q_i\}$ is the set of steady-state solutions of [11], then

$$\dot{n}_1/n_1 = -\lambda_1(n_2^\alpha - q_2^\alpha)/\alpha; \quad \dot{n}_2/n_2 = \lambda_2(n_1^\alpha - q_1^\alpha)/\alpha. \quad [12]$$

The $\alpha = 0$ model is especially interesting since it yields the equations

$$\dot{v}_1 = -\lambda_1 v_2, \quad \dot{v}_2 = \lambda_2 v_1 \text{ or } \ddot{v}_1 = -\lambda_1 \lambda_2 v_1 \quad [13a]$$

with

$$v_j = \log(n_j/q_j) \text{ and } \dot{n}_j = q_j \exp v_j. \quad [13b]$$

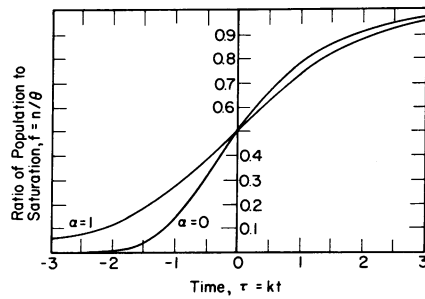


FIG. 1. Curves indicating the difference in population growth between the Gompertz model ($\alpha = 0$) and the Verhulst model ($\alpha = 1$). The reference time is chosen so that at $t = 0$ both curves are at half-saturation level.

The solution of the equations for $\{v_i\}$ are

$$v_1 = \kappa \lambda_2^{-1/2} \cos \omega(t + \delta); v_2 = \kappa \lambda_1^{-1/2} \sin \omega(t + \delta) \quad [14]$$

where the amplitude parameter κ and the phase δ are defined by

$$\kappa^2 = \lambda_2 v_1^2(0) + \lambda_1 v_2^2(0) \quad [15a]$$

$$\tan \omega \delta = \lambda_1^{1/2} v_2(0) / \lambda_2^{1/2} v_1(0) \quad [15b]$$

The spiking character results (6, 7) from substitution of [14] into [13]:

$$n_1 = q_1 \exp \{ \kappa \lambda_2^{-1/2} \cos \omega(t + \delta) \};$$

$$n_2 = q_2 \exp \{ \kappa \lambda_1^{-1/2} \sin \omega(t + \delta) \} \quad [16]$$

κ , which is measured by the deviations of the initial populations from their steady-state values, gives the degree of spiking of [16]. If κ is large, the exponential amplifies the cosine and sine functions more upward when they are positive than it does downward when those functions are negative. As $\kappa \rightarrow \infty$, the sky is the limit for the exponential of positive values of cosine and sine, but the exponential of the negative values cannot fall below zero.

There are two qualitative differences between the curves in Fig. 3, which are plots of [16], and the numerical solutions of the Lotka-Volterra set shown in Fig. 2. n_1 and n_2 of [16] are always out of phase by one-fourth of the period of these functions, while the Lotka-Volterra solutions are out of phase by an amount that diminishes slowly from one-fourth of the period as the initial populations are chosen to be increasingly distant from the steady-state values. Also, the functions [16] are symmetrical around their peaks, while numerical solutions of Lotka-Volterra equations have a slight dissymmetry.

If one takes the original Lotka-Volterra model more seriously than our solvable model, it can be considered as a first approximation to the Lotka-Volterra model, and then perturbation theory can be applied to find corrections. To this end write [7] as

$$d \log (n_1/q_1)/dt = k_1[1 - (n_2/q_2)] \quad [17a]$$

$$d \log (n_2/q_2)/dt = -k_2[1 - (n_1/q_1)] \quad [17b]$$

Then note that since

$$x = \exp (\log x) = 1 + \log x + 1/2(\log x)^2 + \dots, \quad [18]$$

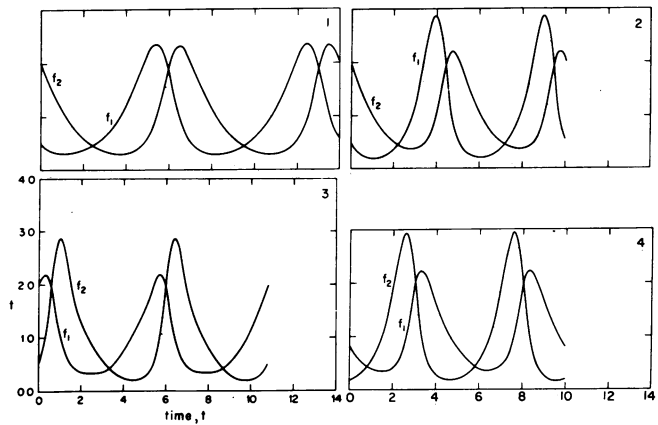


FIG. 2. Time variation of several two-species populations according to the Lotka-Volterra model. The initial conditions are indicated. The values of the parameters k_1 and k_2 for the four cases plotted are (1), $(k_1, k_2) = (1, 1)$; (2), $(1, 2)$; (3), $(1, 2)$; and (4), $(2, 1)$.

Eqs. [17] become (with v_j defined by [13b]),

$$\dot{v}_1 = -k_1 v_2 (1 + 1/2 v_2 + \dots);$$

$$\dot{v}_2 = k_2 v_1 (1 + 1/2 v_1 + \dots) \quad [19]$$

Hence, this is equivalent to the $\alpha = 0$ model equation [12] when second- and higher-order terms in v_i are neglected. These equations can also be written as second-order equations in v_1 and v_2 :

$$\ddot{v}_1 + \omega^2 v_1 = F_1(t) \equiv -1/2 \omega^2 v_1^2 - 1/2 k_1 dv_2^2/dt + \dots \quad [20a]$$

$$\ddot{v}_2 + \omega^2 v_2 = F_2(t) \equiv -1/2 \omega^2 v_2^2 + 1/2 k_2 dv_1^2/dt + \dots \quad [20b]$$

These equations are equivalent to

$$v_j(t) = v_j(0) \cos \omega t + \omega^{-1} v_j'(0) \sin \omega t$$

$$+ \omega^{-1} \int_0^t F_j(\tau) \sin \omega(t - \tau) d\tau \quad [21]$$

Hence, upon substitution of the right-hand side of [20] into

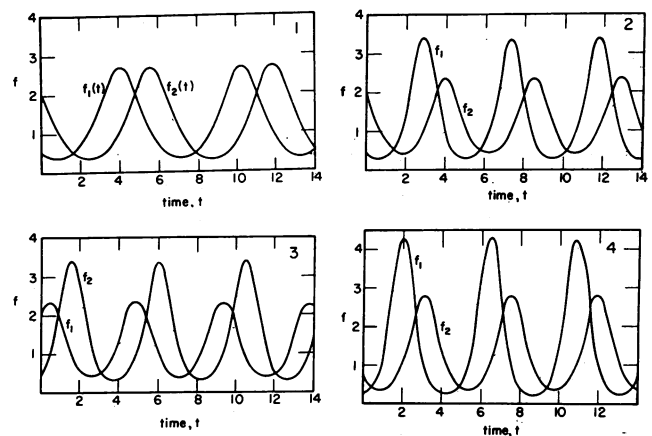


FIG. 3. Time variation of several two-species populations according to the "solvable" $\alpha = 0$ model. The initial conditions are indicated. The values of the parameters α_1 and α_2 for the cases plotted are (1) $(k_1, k_2) = (1, 1)$; (2), $(1, 2)$; (3), $(1, 2)$; and (4), $(2, 1)$.

[21] and an integration by parts, we find that

$$v_1(t) = (\kappa/k_2^{1/2}) \cos \omega(t + \delta) - 1/2\omega \int_0^t \{v_1^2(\tau) \sin \omega(t - \tau) + k_1\omega^{-1}v_2^2(\tau) \cos \omega(t - \tau)\} d\tau \quad [22a]$$

$$v_2(t) = (\kappa/k_1^{1/2}) \sin \omega(t + \delta) - 1/2\omega \int_0^t \{v_2^2(\tau) \sin \omega(t - \tau) - k_2\omega^{-1}v_1^2(\tau) \cos \omega(t - \tau)\} d\tau \quad [22b]$$

$$\kappa^2 = v_1^2(0) + (k_1/k_2)v_2^2(0); \quad \tan \omega\delta = (k_1/k_2)^{1/2}v_2(0)/v_1(0) \quad [22c]$$

If we iterate these equations once (which is equivalent to first-order perturbation theory), we find that

$$(k_2^{1/2}/\kappa)v_1(t) = \cos \omega(t + \delta) + (\kappa/4)\{k_2^{-1/2}(1 - \cos \omega t) + k_1^{-1/2} \sin \omega t\} + (\kappa/12)\{k_2^{-1/2} \cos 2(t + \delta) \omega + 2k_1^{-1/2} \sin 2(t + \delta)\omega - \beta_1 \cos \omega t - \beta_2 \sin \omega t\} \quad [23a]$$

$$(k_1^{1/2}/\kappa)v_2(t) = \sin \omega(t + \delta) - (\kappa/4)\{k_1^{-1/2}(1 - \cos \omega t) - k_2^{-1/2} \sin \omega t\} + (\kappa/12)\{-k_1^{-1/2} \cos 2(t + \delta)\omega + 2k_2^{-1/2} \sin 2(t + \delta)\omega + \beta_2 \cos \omega t - \beta_1 \sin \omega t\} \quad [23b]$$

with

$$\beta_1 = k_2^{-1/2} \cos 2\delta\omega + 2k_1^{-1/2} \sin 2\delta\omega; \quad \beta_2 = k_1^{-1/2} \cos 2\delta\omega - 2k_2^{-1/2} \sin 2\delta\omega \quad [24]$$

The perturbation parameters $\kappa k_i^{-1/2}$ are related to the deviation of the initial conditions from equilibrium. One can iterate again to obtain $v_i(t)$ correct to second order in these parameters. Since the $v_i(t)$ are to be inserted into the exponential expression [13b], these first- and second-order perturbation solutions of the Lotka-Volterra equations have the qualitative features of the nonlinear model, features that would not be so apparent if one merely applied perturbation theory to [7] starting with the linearized equations [8] as the unperturbed equations.

Volterra many-species model

We now extend the ideas discussed above to many variable rate equations by first considering the Volterra generalization of [7] for m species

$$dn_j/dt = k_j n_j + \beta_j^{-1} n_j \sum_{k=1}^m a_{jk} n_k \quad j = 1, 2, \dots, m \quad [1]$$

where $\beta_j^{-1}/\beta_k^{-1}$ represents the exchange rate between species; i.e., the ratio of j 's lost (or gained) to k 's gained (or lost) per unit time. If $\{q_j\}$ represents the set of nonvanishing steady-state solutions of [1], then

$$\beta_j d \log (n_j/q_j)/dt = -\sum_k a_{jk} q_k \{1 - (n_k/q_k)\} \quad [2]$$

Upon application of [18], we find

$$\beta_j \dot{v}_j = \sum_k a_{jk} q_k (v_k + 1/2 v_k^2 \dots) \quad [3]$$

In the Volterra theory, one chooses a_{jk} to be antisymmetrical, $a_{jk} = -a_{kj}$. We restrict ourself to this case and generalize in the next section. Then let

$$U_k \equiv (\beta_k q_k)^{1/2} v_k, \quad \gamma_k = (\beta_k q_k)^{-1/2} \quad [4]$$

$$b_{jk} \equiv a_{jk} (q_j q_k / \beta_j \beta_k)^{1/2}, \quad b_{jk} = -b_{kj}. \quad [5]$$

so that

$$\dot{u}_j = \sum_{k=1}^m b_{jk} u_k (1 + 1/2 \gamma_k u_k) \quad [6]$$

Utilizing ideas used in the two-species case, we introduce model equations

$$\beta_j d \log (n_j/q_j)/dt = -\sum_k a_{jk} q_k \{1 - (n_k/q_k)^\alpha\} / \alpha \quad [7]$$

which, in the case $\alpha = 0$, lead to

$$\beta_j \dot{v}_j = \sum_k a_{jk} q_k v_k \quad \text{with } v = \log n/q; \quad [8]$$

or, using the definitions [4] and [5],

$$\dot{u}_j = \sum_k b_{jk} u_k \quad [9]$$

The solution of this linear set is (5)

$$u_j(t) = \sum_k \sum_l A_{jl} A_{kl}^* u_k(0) \exp \lambda_l t \quad [10]$$

the A_{il} 's being elements of the characteristic vectors of B ,

$$\sum_k b_{ik} A_{kl} = \lambda_l A_{il} \quad \text{with } \sum_l A_{il}^* A_{lj} = \delta_{ij} \quad [11]$$

When B is antisymmetric, the characteristic values $\{\lambda_l\}$ are purely complex and appear in pairs $\pm i\omega_l$. Hence, $v_j(t)$ can be written in the form

$$v_j(t) = \sum_{l=1} f_{jl} \cos \omega_l(t + \delta_{jl}), \quad [12]$$

the $\{f_{jl}\}$ depending on $\{A_j\}$ and $\{v_j(0)\}$. The n_j then have the form

$$n_j(t) = q_j \exp \sum_{l=1} f_{jl} \cos \omega_l(t + \delta_{jl}) \quad [13]$$

for our $\alpha = 0$ model. An important feature of this model is that mode "mixing" or combination occurs in it. This is a special feature of nonlinear problems. Since, when the exponential [13] is expanded, we obtain terms proportional to

$$2 \cos \omega_l(t + \delta_{jl}) \cos \omega_m(t + \delta_{jm}) = \cos[(\omega_l + \omega_m)t + (\omega_l \delta_{jl} + \omega_m \delta_{jm})] + \cos[(\omega_l - \omega_m)t + (\omega_l \delta_{jl} - \omega_m \delta_{jm})],$$

various sum and difference frequencies appear in the expansion of n_j .

If one is not satisfied with our $\alpha = 0$ model and wishes to continue with the Volterra model, then, as was done in the two-species case, [12] can be substituted into the nonlinear term in [3] and first-order perturbation theory can be applied. Since this will be done in detail in the next section for more general rate equations, I will not carry out the required calculations here.

The Volterra model is more general than it might seem from the context of competing species for which it was first introduced. One can imagine situations in which the rate at which one of a number of coupled variables increases is proportional to the magnitude of that variable, and to another quantity that depends on the influence of other variables. Then one would write (7)

$$dN_i/dt = N_i G_i(N_1, N_2, \dots, N_m). \quad i = 1, 2, \dots, m \quad [14]$$

We postulate that the $\{G_i\}$ do not depend explicitly on the time and that a set of positive steady-state populations (Q_1, \dots, Q_m) exist such that

$$G_i(Q_1, Q_2, \dots, Q_m) = 0 \quad i = 1, 2, \dots, m \quad [15]$$

If the functions G_i have a Taylor expansion about steady-state populations, then

$$G_i(N_1, \dots, N_n) = \sum_j (N_j - Q_j) A_i^j + \sum_{jk} (N_j - Q_j)(N_k - Q_k) A_i^{jk} + \dots \quad [16]$$

$$A_i^j \equiv (\partial G_i / \partial N_j)_{ss} \text{ and } A_i^{jk} \equiv (\partial^2 G_i / \partial N_j \partial N_k)_{ss} \quad [17]$$

()_{ss} represents the appropriate quantity in the steady state. Hence,

$$d \log N_i / dt = \sum_j A_i^j (N_j - Q_j) + \sum_{jk} A_i^{jk} (N_j - Q_j)(N_k - Q_k) + \dots \quad [18]$$

If second-order terms are neglected, the resulting equations are similar to Volterra's, except that the a_{ij} 's are not necessarily antisymmetrical. Hence, the Volterra model is a first approximation to situations in which the growth rate of a variable is proportional to its instantaneous value when the population is small and in which a steady-state value exists when there are interactions with other variables.

General rate equations with quadratic nonlinearities

We generalize the above ideas by considering the quadratic rate equations

$$x_i = \sum_j a_i^j x_j + \sum_{jk} a_i^{jk} x_j x_k \quad i = 1, 2, \dots, m \quad [1]$$

Frequently the right-hand side of [1] begins an expansion, perhaps in deviations from a steady state, whose ternary and higher-order rate constants are seldom known explicitly. Hence, it would hardly seem worthwhile to seek solutions of [1] that were correct to higher order than quadratic. That is, one should be satisfied with solving the linear equation obtained by neglecting the quadratic term [1] and then applying first-order perturbation theory to the quadratic term in [1].

If this point of view were taken seriously, certain basic nonlinear effects such as saturation and spiking and higher-order mode mixing would not become so apparent. The program outlined below, motivated by our study of the Volterra model, provides a solution of [1] that yields the desired nonlinear effects and that is quantitatively correct to the order of the quadratic terms in [1].

We first neglect the quadratic terms in [1] and rewrite the linear equations in matrix form $\dot{x} = Ax$. Suppose that A (with characteristic values $\{\lambda_j\}$) can be diagonalized by T . Then if $y = T^{-1}x$, the components of y satisfy $\dot{y}_i = \lambda_i y_i$. With the same transformation, [1] becomes

$$\dot{y}_i = \lambda_i y_i + \sum_{jk} \Gamma_i^{jk} y_j y_k \quad [2]$$

with the new rate constants Γ_i^{jk} depending on the a_i^j and a_i^{jk} . We rewrite [2] as

$$d \log y_i / dt = \lambda_i + \sum_{jk} \Gamma_i^{jk} y_j y_k / y_i \quad [3]$$

If a set of steady-state values of $\{y_i\}$, say $\{q_i\}$, exist, then

$$d \log (y_i / q_i) / dt = \sum_{jk} \Gamma_i^{jk} (q_j q_k / q_i) \left\{ \frac{y_j y_k q_i}{q_j q_k y_i} - 1 \right\} \quad [4]$$

We note that if (y/q) is close to 1,

$$(y/q) = \exp[\log(y/q)] = 1 + \log(y/q) + \frac{1}{2}[\log(y/q)]^2 + \dots \quad [5]$$

Hence, if we let $y_j = q_j \exp v_j$, substitute this expression into [4], and neglect terms of order v^2 or higher, we find

$$\dot{v}_i = -\eta_i v_i + \sum_j \alpha_i^j v_j \quad [6a]$$

$$\eta_i = \sum_{jk} (q_j q_k / q_i) \Gamma_i^{jk}, \quad \alpha_i^j = \sum_k (q_j q_k / q_i) (\Gamma_i^{jk} + \Gamma_i^{kj}) \quad [6b]$$

Since [6] is linear, it can be solved by standard methods.

Had we retained second-order terms in deriving [6], we would have found

$$\dot{v}_i = -\eta_i v_i + \sum_j \alpha_{ij} v_j + \sum_{jk} \Gamma_i^{jk} \{ (v_j + v_k)^2 - v_i(v_j + v_k - \frac{1}{2}v_i) \} + \dots \quad [7]$$

In matrix form, with $F(t)$ representing the quadratic terms of [7],

$$\dot{V} = -AV + F\{V(t)\} \quad [8]$$

Let us suppose that the matrix A can be diagonalized by S . Then

$$S\dot{V} = -SAS^{-1}SV + SF\{V(t)\} \quad [9]$$

Hence, if we define $U = SV$ and $B = SAS^{-1}$, and assume that the characteristic values of B (and, of course, S) are λ_j ,

$$\dot{u}_j = -\lambda_j u_j + [SF\{V(t)\}]_j \quad [10]$$

from which we deduce that

$$u_j(t) = u_j(0) \exp(-t\lambda_j) + \int_0^t [TF\{V(\tau)\}]_j \exp\{-\lambda_j(t - \tau)\} d\tau \quad [11]$$

Since $F(t)$ is a function of V that is related to the u_j through $V = S^{-1}U$, this equation can be iterated to yield an expression to $u_j(t)$ that has a first-order perturbation correction. If the elements of S and S^{-1} are, respectively, $\{S_{jk}\}$ and $\{S_{jk}^{(-1)}\}$, then

$$v_i(t) = \sum_j S_{ij}^{(-1)} u_j(t) \quad [12]$$

and the first-order perturbation solution of [2] follows from [12].

One of the missing features of our perturbation theory is that under initial conditions far from steady state, the normal mode frequencies may depend on the initial conditions. I have not incorporated this into this analysis.

The scheme presented in this section would not be uniformly applicable to all equations of type 1 under all possible initial conditions. My discussion should be considered as a strategy that might be tried in exploring [1]. It is an example of the general strategy of seeking a "solvable" set of nonlinear equations whose solutions can be expected to have qualitative features similar to those of a set of interest. The set of interest can then be considered as a perturbed version of the solvable set. A number of other solvable rate equations are given in refs. 7 and 8. We conclude our discussion with a solvable class of nonlinear rate equations not mentioned in those references.

Faltung or resultant-type rate equations

The solvable nonlinear models considered above were solved by transformations in the dependent variables. This section considers another class of solvable rate equations that might be used as first approximations to certain nonlinear rate equations.

Let $F(k,t) \equiv F(k)$ be a driving force and $U(k,t) \equiv U(k)$ a function satisfying

$$\dot{U}(k) = \int_{-\infty}^{\infty} S_1(k - k')dk' + \iint_{-\infty}^{\infty} S_2(k - k' - k'')U(k')U(k'')dk'dk'' + F(k) \quad [1]$$

A special example of this equation is the Smoluchowski coagulation equation (also used by Shumann in the theory of fog formation):

$$\frac{dx(k,t)}{dt} = k \int_{-\infty}^{\infty} x(k - k',t)x(k',t)dk' - 2kN(t)x(k,t) \quad [2]$$

This corresponds to the rate at which the number of particles $x(k,t)$ of mass k at time t increases due to collision of particles of mass $(k - k')$ with those of mass k . The second term on the right is a loss term, due to collision of particles of mass with those of any other size, $N(t)$ being the total number of particles. Eq. [2] is a special case of [1] with $F \equiv 0$, $S_1(k - k') = kN(t)\delta(k - k')$ and $S_2(k) = \delta(k)$. The linear form with $S_1(k) = D\delta''(k)$ leads to a diffusion-type equation.

Eq. [1] can be reduced to an ordinary differential equation by introduction of Fourier transforms

$$\left. \begin{matrix} u(\theta,t) \\ f(\theta,t) \\ s_j(\theta,t) \end{matrix} \right\} = \int_{-\infty}^{\infty} dk e^{ik\theta} \left\{ \begin{matrix} U(k,t) \\ F(k,t) \\ S_j(k,t) \end{matrix} \right\} \quad [3]$$

Upon application of the Fourier faltung theorem, we find (with $u(\theta,t) \equiv u$, etc.)

$$\dot{u} = f + s_1u + s_2u^2 \quad [4]$$

which is of the Riccati type. Hence, if we define v by $u = s_2^{-1}(\log v)$, and if S_2 is chosen to be independent of time (even though S_1 and F may depend explicitly on t), one finds that

$$\dot{v} - s_1v + s_2fv = 0. \quad [5]$$

If w is defined by

$$v = w \exp^{1/2} \int_a^t s_1(\theta,\tau)d\tau, \quad [6]$$

then w satisfies an equation that resembles the Schrodinger equation

$$\ddot{w} + [-1/4s_1^2 + 1/2s_1 + s_2f(\theta,t)]w = 0. \quad [7]$$

If $s_1(\theta,t)$ and $f(\theta,t)$ are chosen to be functions of t for which [7] has a solution in terms of classical special functions, then our problem is reduced to quadratures. In this case w would be de-

termined, so that from [6] v would become known. A specific case of interest might be one with s_1 independent of time and $f(\theta,t) = g(\theta) \cos 2\omega t$. This is typical of a periodic driving force. Eq. [7] then has the Mathieu form (with $z = w t$)

$$d^2w/dz^2 + (a + 16q \cos 2z)w = 0$$

where

$$a = 1/2w^2s_1(1 - 1/2s_1) \text{ and } 16q = w^2s_2q(\theta).$$

Then the solution of [7] could be expressed in Mathieu functions (9).

To investigate a system response to a pulse, one might choose $f(\theta,t) = l(l + 1)\gamma^2 \text{sech}^2\gamma t$, which has a peak at $t = 0$. The solutions of [7] are elementary (10) for some values of l and in terms of hypergeometric functions (11) for arbitrary l . The explicit form of [7] in this case is

$$\ddot{w} + [1/2s_1(1 - s_1) + s_2l(l + 1)\gamma^2 \text{sech}^2\gamma t]w = 0.$$

In order to establish some idea of the form of the solution, suppose that $F(k,t) \equiv 0$. Then $f(\theta,t) \equiv 0$ in [4] and the transformation $v = 1/p$ yields

$$-dp/dt = s_1p + s_2 \quad [8]$$

which is solvable even when s_1 and s_2 are both functions of time. After solution and Fourier inversion, one finds that (7)

$$U(k,t) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \frac{u(\theta,0) \exp(-ik\theta)d\theta}{I(\theta,t) - u(\theta,0)J(\theta,t)} \quad [9]$$

where

$$\begin{aligned} u(\theta,0) &= \int_{-\infty}^{\infty} e^{ik\theta}U(k,0)dk, \quad I(\theta,t) = \exp - \int_0^t s_1(\theta,\tau)d\tau \\ J(\theta,t) &= \int_0^t s_2(\theta,t') \exp - \int_{t'}^t s_1(\theta,\tau)d\tau dt'. \end{aligned} \quad [10]$$

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1. Verhulst, P. F. (1838) *Correspondence Mathematique et Physique 10*; reprinted in (1965) *Readings in Ecology*, ed. Kormondy, E. J. (Prentice-Hall, Englewood Cliffs, N.J.).
2. Gompertz, B. (1825) *Phil. Trans. Roy. Soc.* 115, 513.
3. Lotka, A. J. (1924) *Elements of Physical Biology*; reprinted (1956) as *Elements of Mathematical Biology* (Dover).
4. Volterra, V. (1931) *Lecon de la theorie mathematique de la lutte pour la vie* (Gauthier Villars, Paris).
5. Goel, N. S., Maitra, S. C. & Montroll, E. W. (1971) *Rev. Mod. Phys.* 43, 241-276.
6. Montroll, E. W. (1972) *Some Math. Probl. Biol. IV*, 101-143.
7. Montroll, E. W. (1972) *Proc. of IUPAP Stat. Mech. Conf.* (Univ. of Chicago Press).
8. Montroll, E. W. (1967) *Lectures in Theoretical Physics* (Univ. of Colorado), Vol. XA, pp. 531-573.
9. Whittaker, E. T. & Watson, G. N. (1962) *A Course in Mathematical Analysis* (Cambridge Univ. Press), 4th Ed.
10. Montroll, E. W. (1970) *J. Math. Phys.* 11, 635-648.
11. Landau, L. D. & Lifshitz, E. M. (1965) *Quantum Mechanics* (Pergamon Press, N.Y.).