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NONLINEAR ASPECTS OF COMPETITION BETWEEN THREE SPECIES*

ROBERT M. MAY† AND WARREN J. LEONARD‡

Abstract. It is shown that for three competitors, the classic Gause–Lotka–Volterra equations possess a special class of periodic limit cycle solutions, and a general class of solutions in which the system exhibits nonperiodic population oscillations of bounded amplitude but ever increasing cycle time. Biologically, the result is interesting as a caricature of the complexities that nonlinearities can introduce even into the simplest equations of population biology; mathematically, the model illustrates some novel tactical tricks and dynamical peculiarities for 3-dimensional nonlinear systems.

1. Introduction. Even the simplest equations of population biology are, by and large, nonlinear. Consequently, the possible stable equilibrium solutions of these equations are not necessarily stable points, as they must be in linear systems, but can be stable limit cycles.

For example, a single population whose continuous growth is described by a time-delayed logistic differential equation (Hutchinson (1948)) has as its asymptotic solution either a stable constant value or a limit cycle, depending on whether the time-delay is short or long compared with the natural time scale of the system (May (1973a)). Similarly, a single population of nonoverlapping generations, whose discrete growth steps obey some biologically sensible density-dependent difference equation, asymptotically settles either to a stable equilibrium point or to some stable cycle, again depending on whether the built-in one-generation time delay in the operation of the regulatory mechanisms is relatively short or long (Van der Vaart (1973), May et al. (1974)). Kolmogorov (1936) showed in general terms that most differential equations modeling one-predator-one-prey situations may be expected asymptotically to show either stable point or stable limit cycle behavior, and May (1972), (1973a) demonstrated that Kolmogorov's general result applied specifically to essentially all the predator-prey models to be found in the ecological literature. (In all these examples, one can also construct pathological neutrally stable periodic solutions, usually by choosing growth rates whose density dependence exhibits discontinuities. Such structurally unstable models have little biological significance; see May (1973b), Lewontin (1969)).

The nonlinear analysis of these examples usually rests on the Poincaré–Bendixson theorem (see, e.g., Rosen (1970)), itself derived from Jordan's observation that a closed curve divides a 2-dimensional domain into an inside and an outside. This basis is explicit in the 2-dimensional predator-prey discussions, and by a clever trick can be extended to many 1-dimensional differential-delay equations (Kaplan and Yorke (1975)).

For two *competing* species, 1 and 2 say, the conventional model, namely the quadratically nonlinear Gause–Lotka–Volterra (GLV) equations, is (in contrast with the above examples) rather dull. The asymptotic behavior is convergence to

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one or other of the 4 possible equilibrium points (1 and 2 coexisting; 1 alone; 2 alone; both vanishing), depending on the relative magnitudes of the competition coefficients.

The analogous GLV differential equations for *three* competing populations, labeled 1, 2 and 3, are more interesting. Previous discussions (e.g., Rescigno (1968)) have been confined to a classification of the parameter values for which the system settles down to a particular one of the 8 possible equilibrium points (namely, all three coexisting, 3 combinations of two coexisting, 3 single populations, all three vanishing). But, unlike the two-species case, there remain combinations of the competition coefficients such that the system does not converge to any one of these 8 equilibrium points.

As we shall see below, a nonlinear study of this domain of parameter space reveals both an exceptional class of stable periodic limit cycle solutions and a wider class of asymptotic solutions in which the system cycles from being composed almost wholly of population 1, to almost wholly 2, to almost wholly 3, back to 1, but with the time to complete the cycle becoming longer and longer (being proportional to the length of time the system has been running), and with the system coming in turn ever closer to the points with 1 alone, 2 alone and 3 alone, yet never actually converging on any one point (see Figs. 3, 4, 5).

This paper explores these odd and explicitly nonlinear features of the three-species competition equations.

Biologically, the study is of interest as a mathematical morality play emphasizing the remarkable effects the nonlinearities can produce even in the most straightforward equations of population biology. Cycles produced by pure competition have not previously been noted, and indeed cannot be produced from the conventional GLV differential equations for competition unless at least three competitors are present.

Mathematically, the study is of interest partly because it illustrates some tactical tricks which can be useful in certain 3-dimensional systems (for which the powerful, but 2-dimensional, Poincaré–Bendixson techniques, which underpin most previous nonlinear studies in population biology, are no longer available), and partly because the general asymptotic behavior typified by Figs. 3, 4, 5, namely cycles whose length increases as time goes on, is worth noting.

Subsequent to the present work, and quite independent of it, Gilpin (1975) has made a similar (mainly numerical) study of oscillatory phenomena in models with three or more competitors. His paper has a much more biological focus: it and the present work complement each other.

In § 2, we outline the GLV model for three competitors and indicate conditions such that none of the 8 possible equilibrium points are stable. In § 3, we consider a special case ($\alpha + \beta = 2$) which leads to a 1-parameter family of stable periodic limit cycles. In § 4, we treat the more general case ($\alpha + \beta > 2$) which leads to cycles of ever lengthening period as described above. Some mathematical details relevant to § 4 are in the Appendix. A brief discussion of the biological implications of these results comprises § 5.

2. Three competitors. The GLV equations describing the dynamics of n competing populations consist of n first order differential equations:

$$\frac{dN_i(t)}{dt} = r_i N_i(t)\left[1 - \sum_{j=1}^{n} \alpha_{ij} N_j(t)\right]. \tag{1}$$

Here $N_i(t)$ is the number of individuals in the ith population at time t, r_i is the intrinsic growth rate of the ith population, and the α_{ij} are competition coefficients measuring the extent to which the jth species affects the growth rate of the ith.

For three competitors, $n = 3$, there are 12 parameters (9 elements of the matrix $\boldsymbol{\alpha}$, 3 of the vector $\mathbf{r}$), and although 4 parameters may be absorbed by renormalizing the 3 populations and the time t, there remain 8 disposable parameters characterizing the system. As discussed in the introduction, there are 8 possible equilibrium points, where $dN_i/dt = 0$, and various values of the parameters $\boldsymbol{\alpha}$ and $\mathbf{r}$ can lead to one or other of these points being stable. However, there remain regions of parameter space such that none of these 8 points are stable, yet where the populations asymptotically have bounded values: this circumstance has not previously been discussed.

In order to give a manageable exposition, we henceforth reduce the number of parameters in the three-competitors system by making the symmetry assumptions that (i) $r_1 = r_2 = r_3 = r$; (ii) with respect to competition, 2 affects 1 as 3 affects 2 as 1 affects 3, i.e., $\alpha_{12} = \alpha_{23} = \alpha_{31} = \alpha$; (iii) similarly $\alpha_{21} = \alpha_{32} = \alpha_{13} = \beta$. Furthermore, we may rescale the populations N_i so that effectively $\alpha_{ii} = 1$, and rescale t so that in effect $r = 1$ (which embodies the assumption that $r > 0$), to arrive at

$$\frac{dN_1}{dt} = N_1[1 - N_1 - \alpha N_2 - \beta N_3], \tag{2a}$$

$$\frac{dN_2}{dt} = N_2[1 - \beta N_1 - N_2 - \alpha N_3], \tag{2b}$$

$$\frac{dN_3}{dt} = N_3[1 - \alpha N_1 - \beta N_2 - N_3]. \tag{2c}$$

It is plausible that qualitative features of these equations will remain true in the more general unsymmetric case. We discuss this in § 5.

The possible equilibrium solutions may be expressed as points in the 3-dimensional population space: they are the points $(0, 0, 0)$; 3 single-population solutions of the form $(1, 0, 0)$; 3 two-population solutions of the form $(1 - \alpha, 1 - \beta, 0)/(1 - \alpha\beta)$; and the three-species equilibrium $(1, 1, 1)/(1 + \alpha + \beta)$. It is in general a routine, although often algebraically messy, matter to study the stability of such equilibrium points (via the Routh–Hurwitz criteria, or otherwise). In particular, for $r > 0$ the three-species equilibrium is stable if and only if all eigenvalues of the matrix

$$\begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{pmatrix}$$

have positive real parts. This matrix is so-called circulant, and its eigenvalues can be written down (see the general formula in, e.g., May (1973a, p. 198, (A.30))):

$$\lambda_1 = 1 + \alpha + \beta,$$
$$\lambda_{2,3} = 1 - (\alpha + \beta)/2 \pm i(\sqrt{3}/2)(\alpha - \beta).$$

Thus for $\alpha > 0$ and $\beta > 0$ the necessary and sufficient condition for neighborhood stability is $\alpha + \beta < 2$.

For $r > 0$, the dynamical properties of the system of equations (2) as a function of the two parameters α and β are summarized in Fig. 1. As a result of the assumption $r > 0$, neither $(0, 0, 0)$ nor any two-species equilibrium point is stable; there is a three-species stable point if $\alpha + \beta < 2$, and convergence to one of the single-species equilibrium points (which one depends on the initial conditions) if both $\alpha > 1$ and $\beta > 1$. For $\alpha + \beta \geqq 2$ and either $\alpha < 1$ or $\beta < 1$, no stable point exists. We proceed to study this case.

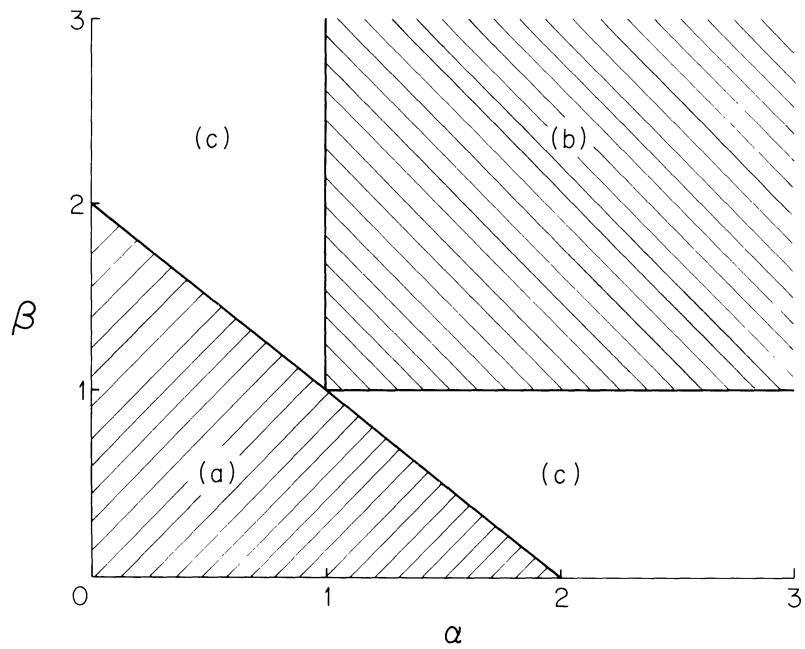

FIG. 1. *The figure shows the stability properties of* (2) *as a function of the competition parameters* α *and* β. *In the domain* (a) *the stable equilibrium point is that with all three populations present*; *in the domain* (b) *the* 3 *single-species equilibrium points* (1, 0, 0), (0, 1, 0) *and* (0, 0, 1) *are all stable, and which one the system converges to depends on the initial conditions*; *in the domain* (c) *there is* no *asymptotically stable equilibrium point, and cyclic solutions of the kind depicted in Figs.* 2–5 *ensue*.

3. The special case $\alpha + \beta = 2$. We first consider (2) for the case $\alpha + \beta = 2$, which divides the three-species equilibrium point from the behavior discussed in § 4 below (see Fig. 1). Although this 1-dimensional class of α, β-values is of measure zero in the α, β-plane, it gives rise to an interesting family of special solutions.

First, define

$$N_T(t) \equiv N_1(t) + N_2(t) + N_3(t). \tag{3}$$

For $\alpha + \beta = 2$, summing (2a), (2b), (2c) gives for N_T the simple equation

$$dN_T/dt = N_T - N_T^2. \tag{4}$$

This has the general solution

$$N_T(t) = \frac{N_T(0)}{N_T(0) + [1 - N_T(0)]\, e^{-t}}. \tag{5}$$

The asymptotic solution is clearly

$$N_T(t \to \infty) \to 1. \tag{6}$$

That is, the asymptotic solution lies on the *plane* $N_1 + N_2 + N_3 = 1$ in the 3-dimensional population space; this plane is illustrated in Fig. 2.

Second, notice that (2a), (2b), (2c) can be rewritten in the form

$$\frac{d(\ln N_i)}{dt} = 1 - \sum_{j=1}^{3} \alpha_{ij} N_j. \tag{7}$$

Adding the three equations in this form, with $\alpha + \beta = 2$, leads to

$$\frac{d}{dt}[\ln (N_1 N_2 N_3)] = 3 - 3N_T. \tag{8}$$

For notational convenience we introduce $P(t)$, the product of the three populations at time t:

$$P(t) \equiv N_1(t) N_2(t) N_3(t). \tag{9}$$

Equation (8), in conjunction with (4), then reads

$$\frac{d}{dt}[\ln P(t)] = 3\frac{d}{dt}[\ln N_T(t)]. \tag{10}$$

Integrating,

$$\frac{P(t)}{P(0)} = \left\{ \frac{N_T(t)}{N_T(0)} \right\}^3. \tag{11}$$

Asymptotically, $P(t)$ thus tends to the constant value

$$P(\infty) \to C \equiv P(0)[N_T(0)]^{-3}. \tag{12}$$

That is, as $t \to \infty$ the solution to (2) lies on the *hyperboloid* $N_1 N_2 N_3 = C$ in the 3-dimensional population space. There is a 1-dimensional family of such hyperboloids, depending on the constant C of (12), which in turn depends on the initial conditions.

Combining these results, the asymptotic solution of (2) for $\alpha + \beta = 2$ is seen to lie at the intersection of the above plane and hyperboloid, which is a *circle* in the 3-dimensional population space. Thus any initial point $(N_1(0), N_2(0), N_3(0))$ in the population space will tend towards a periodic limit cycle, as illustrated in Fig. 2. These periodic cycles constitute a 1-dimensional family, specified by the constant C of (12).

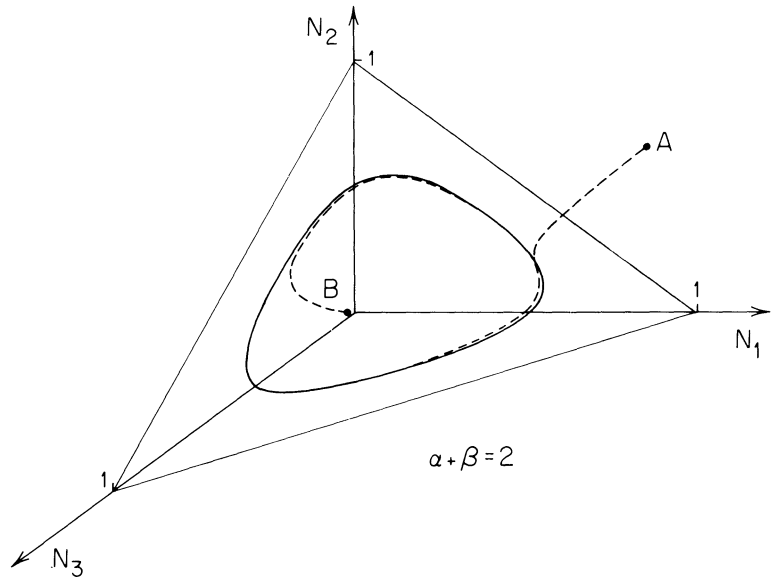

FIG. 2. *This figure depicts the 3-dimensional N_1, N_2, N_3 population space for $\alpha = 0.8$ and $\beta = 1.2$ (so that $\alpha + \beta = 2$), and shows the limit cycle (solid curve) at the intersection of the plane $N_1 + N_2 + N_3 = 1$ and one particular hyperboloid, namely $N_1N_2N_3 = 0.02$. The dashed lines indicate the manner in which the system asymptotically tends to this limit cycle from the initial point $A = (1.0, 0.8, 0.2)$, and from the point $B = (0.01, 0.04, 0.05)$; for both these points the constant in (12) is clearly $C = 0.02$.*

4. The general case $\alpha + \beta > 2$ and $\alpha < 1$. We now consider the solution of (2) for the more general glass of α, β-values represented by the domain (c) in Fig. 1. For definiteness we take $\beta > 1 > \alpha$, although all the results apply, mutatis mutandis, to $\alpha > 1 > \beta$.

At the outset, it is useful to define the positive quantity γ:

$$\gamma \equiv \alpha + \beta - 2. \tag{13}$$

The equation for $N_T(t)$ (see (3)), obtained by adding (2a), (2b), (2c), is now

$$\frac{dN_T}{dt} = N_T(1 - N_T) + \gamma(N_1N_2 + N_2N_3 + N_3N_1). \tag{14}$$

Likewise, the equation for $P(t)$ (see (9)) obtained by adding the three equations of the form (7) is no longer simply (8), but is

$$\frac{d[\ln P]}{dt} = -\gamma + (3 + \gamma)(1 - N_T). \tag{15}$$

We now assume the product terms of order N_1N_2, etc., in (14) asymptotically make a negligible contribution, with the consequence that for large t,

$$N_T \to 1. \tag{16}$$

This assumption is justified in the Appendix. Then (15) has the asymptotic solution

$$\ln [P(t)/P(t_0)] \to -\gamma(t - t_0). \tag{17}$$

That is,

$$P(t) \to k\, e^{-\gamma t}, \tag{18}$$

where k is a constant which depends on the early history of the system.

Note the character of the asymptotic solution. It lies on the plane $N_1 + N_2 + N_3 = 1$, but (in contrast to the case $\alpha + \beta = 2$) the product of the three populations becomes exponentially small as time goes on. The system thus comes ever closer to the lines $N_1 + N_2 = 1, N_2 + N_3 = 1, N_3 + N_1 = 1$ (see Fig. 3); however, it never actually converges on any single point, because there are *no* asymptotically stable points for α, β-values in the domain (c) of Fig. 1.

To understand what is happening for large t, consider (2) in the neighborhood of the point $(1, 0, 0)$. Here N_1 may be regarded as being approximately unity and, from (18), N_2 and N_3 as being exponentially small. Thus, approximately,

$$\frac{dN_1}{dt} \simeq (1 - N_1) - \alpha N_2 - \beta N_3, \tag{19a}$$

$$\frac{dN_2}{dt} \simeq -(\beta - 1)N_2, \tag{19b}$$

$$\frac{dN_3}{dt} \simeq (1 - \alpha)N_3. \tag{19c}$$

All the rates of change are exponentially small. From (16) and (18) we remark that the system tends to move in towards the point $(1, 0, 0)$ along the line $N_1 + N_2 \simeq 1$ (with N_3 exponentially small), and to move out from this point along the line $N_3 + N_1 \simeq 1$ (with N_2 exponentially small); moreover, we note that the regime of approach toward the point is divided from departure from it at the symmetric point where, from (18),

$$N_2 \simeq N_3 \simeq k^{1/2}\, e^{-1/2\gamma t} \equiv \mu(t). \tag{20}$$

Thus the time spent approaching the neighborhood of $(1, 0, 0)$, τ_{in}, may be crudely estimated by integrating (19b) from $N_2 \simeq 1/2$ to $N_2 \simeq \mu(t)$:

$$\ln\left[2k^{1/2}\, e^{-1/2\gamma t}\right] \simeq -(\beta - 1)\tau_{\text{in}}. \tag{21}$$

That is, for $t \gg 1$,

$$\tau_{\text{in}} \simeq \frac{\gamma t}{2(\beta - 1)}, \tag{22}$$

where t is the total time elapsed up to the point where the system attains the neighborhood of $(1, 0, 0)$ in this particular cycle. Similarly, the time spent departing the neighborhood of $(1, 0, 0)$, τ_{out}, may be roughly estimated by integrating (19c) from $N_3 \simeq \mu(t)$ to $N_3 \simeq 1/2$:

$$\tau_{\text{out}} \simeq \frac{\gamma t}{2(1 - \alpha)}. \tag{23}$$

Therefore the total time spent in the neighborhood of such a point in any one cycle, $\tau = \tau_{\text{in}} + \tau_{\text{out}}$, is roughly

$$\tau \simeq \frac{\gamma(\beta - \alpha)}{2(\beta - 1)(1 - \alpha)} t, \tag{24}$$

On the other hand, the time spent transversing the 3 lines $N_1 + N_2 = 1$, etc., outside the exponentially close neighbourhood of the 3 points (1, 0, 0), etc., may be similarly roughly estimated as constant, independent of t. Therefore as $t \to \infty$, only a time of relative order $1/t$ is spent outside the immediate neighborhoods of the 3 points.

In short, the system moves in population space from the neighborhood of the point where only species 1 is present, (1, 0, 0), to the neighborhood of the point (0, 0, 1), to the neighborhood of (0, 1, 0), back to (1, 0, 0), and so on. Asymptotically, the time spent in the vicinity of any one point τ is proportional to the total time elapsed up to that stage t: this relation is described roughly by (24). The total time spent in completing one cycle is likewise proportional to the length of time the system has been running.

These approximate analytic insights are borne out by the exact numerical results displayed in Figs. 3, 4, 5. Figure 3 aims to depict the 3-dimensional population space, and shows the system converging onto the plane $N_T = 1$, and more specifically onto the lines $N_1 + N_2 = 1$, etc. Figures 4 and 5 follow a particular population, $N_1(t)$; in Fig. 4 the time scale is linear, while in Fig. 5 it is logarithmic, the better to illustrate the behavior described above. These figures are for $\beta = 1.3$ and $\alpha = 0.8$, whence $\gamma = 0.1$. Notice the estimate (24), namely $\tau \simeq 0.42t$, is in good agreement with the exact numerical results.

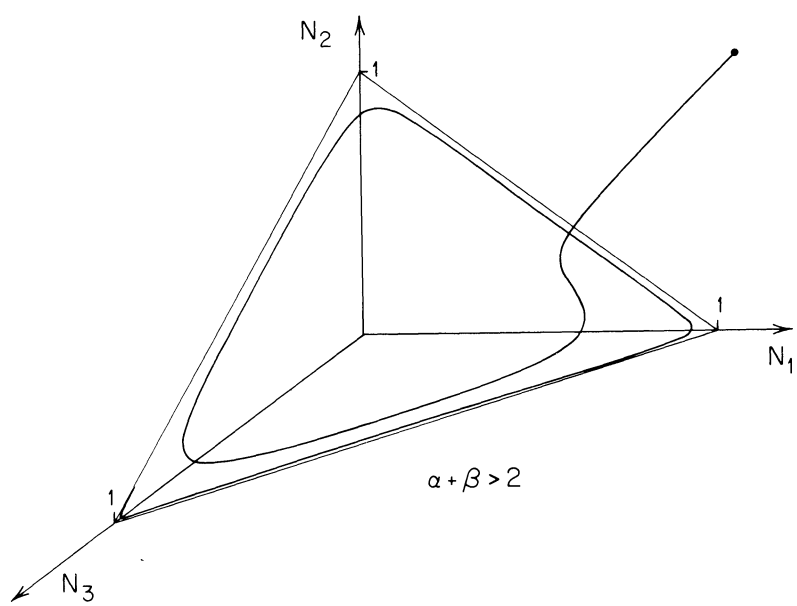

FIG. 3. *This figure illustrates the behavior of the three competing populations N_1, N_2, N_3, obeying (2) in the case $\alpha = 0.8$ and $\beta = 1.3$, so that $\alpha + \beta > 2$. The system appears asymptotically to move ever closer to an orbit carrying it along the lines $N_2 + N_1 = 1$, $N_1 + N_3 = 1$, $N_3 + N_2 = 1$ (that is, along the lines where the plane $N_1 + N_2 + N_3 = 1$ intersects the planes $N_3 = 0$, $N_2 = 0$, $N_1 = 0$, respectively.*

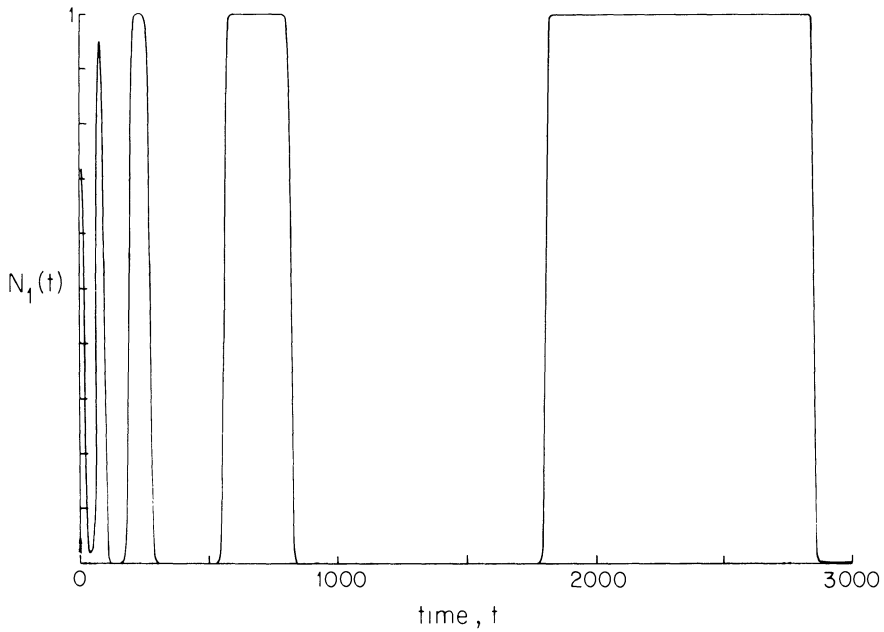

FIG. 4. *The behavior of one of the three populations, namely $N_1(t)$, as a function of time t for $\alpha = 0.8$ and $\beta = 1.3$. (The initial condition is the point* (0.6, 0.6, 0.1).) *This figure illustrates the nonperiodic cyclic behavior discussed in the text.*

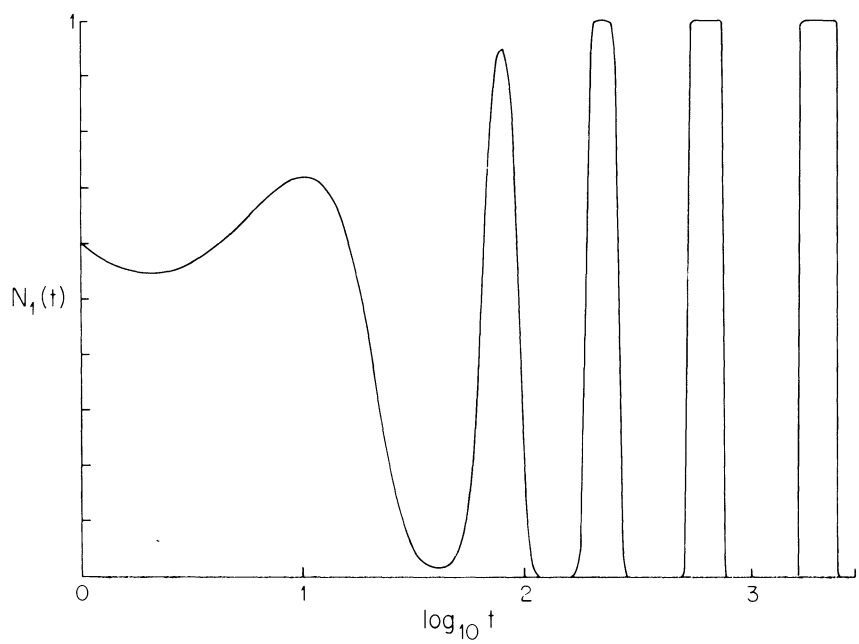

FIG. 5. *This figure repeats the information in Fig.* 4, *but using a logarithmic scale for the time axis, to illustrate the way the cycle length is proportional to how long the system has been running.*

5. Discussion. The mathematical intuition derived from comparatively realistic 1- and 2-dimensional models in population biology (time-delayed population growth and predator-prey models) leads one often to expect either stable equilibrium points or stable periodic limit cycles. However, in the simplest of 3-dimensional systems, namely three competitors obeying the classical GLV equations, the broad class of solutions typified by Figs. 4 and 5 are outside this intuition, and as such are worth noting.

(One of the referees, G. F. Oster, drew to our attention Smale's (1974) recent general result pertaining to equations of the form

$$\frac{dx_i}{dt} = x_i M_i(x_1, x_2, \cdots, x_n),$$

where $i = 1, 2, \cdots, n$ and $n \geqq 3$. Assuming the biologically reasonable constraints that $x_i \in R^n_+$, that $\partial M_i/\partial x_j < 0$ for all i and j, and that $M_i \to 0$ as $x_j \to \infty$, Smale showed the system can exhibit *arbitrary* dynamical behavior (in a generic sense). As Oster reasonably remarks, "In the light of this general result, the example in this paper is not too surprising.")

Biologically, the behavior illustrated in Figs. 4 and 5 is nonsense. Mathematically, for continuous variables $N_i(t)$, the system never asymptotically attains any of the points (1, 0, 0), (0, 1, 0), (0, 0, 1). However, once it is conceded that the variables $N_i(t)$ represent animals, and therefore cannot fall below unity, it is clear that the system will, after a few cycles, converge on some single population, extinguishing the other two. What remains interesting about the analysis is the general observation that nonlinearities can produce nonperiodic cyclic phenomena of the kind depicted in Figs. 2–5.

Finally, we note that the values of the competition coefficients α, β which lead to cycles (namely the region (c) in Fig. 1) may be seen to correspond to the biological circumstance where in purely pairwise competition 1 beats 2, 2 beats 3, and 3 beats 1. Such circumstances are not implausible. It is this intransitivity in the pairwise competition which underlies the cyclic behavior; the phenomenon clearly requires at least three competitors, which is why it cannot occur in models with two competitors. This general type of phenomenon also arises in the theory of voting, where it is for obvious reasons known as the "voting paradox", and enjoys a rich literature (see, e.g., Arrow (1951), Black (1958)); the intransitive, cyclic preference order can arise quite naturally upon aggregating voters' preferences which individually are perfectly transitive. Although earlier work on the "voting paradox" made various symmetry assumptions akin to those which reduce (1) to (2), more recent work has shown the phenomenon to be a robust one, not qualitatively dependent on such simplifying assumptions (May, (1971)).

Appendix. We outline a self-consistent justification of the assumption expressed in (16), namely that for $t \gg 1$ the product terms in (14) are on the average negligible.

Write $N_T(t) = 1 + x(t)$. Then, neglecting terms of order x^2, we see that (14) reads

$$\frac{dx}{dt} = -x + \gamma(N_1N_2 + N_2N_3 + N_3N_1). \tag{A.1}$$

Now, as discussed in the analysis leading up to the approximate relations (22), (23), (24), the product N_1N_2 asymptotically will be exponentially small (of general order $\exp[(-1/2)\gamma t]$ or smaller) *except* as the system is traversing the line $N_1 + N_2 \simeq 1$ en route from the point (0, 1, 0) to the point (1, 0, 0). Along the line (outside the immediate neighborhood of the endpoints), the product N_1N_2 will be less than, but of the general order of, unity. As discussed following (24), the time so spent traversing this line is asymptotically constant, in contrast to the total cycle time which scales as t: consequently the quantity N_1N_2 when *averaged* over a complete cycle at time t has a value of order $1/t$. Identical considerations apply to N_2N_3 and N_3N_1, so that, averaging over a cycle at time $t \to \infty$,

$$\frac{dx}{dt} + x = O(\gamma/t). \tag{A.2}$$

Integrating, for $t \to \infty$,

$$x(t) = O\left[\gamma\, e^{-t} \int^t e^s\, ds/s\right] = O(\gamma/t). \tag{A.3}$$

This self-consistent argument thus leads to (16).

A more technically detailed version of this argument may be given, to the same end. The exact numerical results of Figs. 4 and 5 also bear out the above remarks.

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