MODELS FOR AGE-SPECIFIC INTERACTIONS IN A PERIODIC ENVIRONMENT

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Abstract. In 1954 Hutchinson and Slobodkin suggested that populations can be viewed as feedback systems that could resonate in response to environmental fluctuation with a frequency of approximately one generation time. In this paper we pursue this observation by constructing several mathematical models based on the demographic equations governing population age structure. The existence of this and several other effects of ecological importance are investigated for populations coupled by age-specific interactions.

Key words: Age-specific interaction; age structure; distributed parameter model; model; oscillations; parasite-host system; partial differential equations; periodic environment; resonance.

INTRODUCTION

One of the principal challenges facing contemporary ecology is to understand the dynamics of natural populations. Since the pioneering work of Volterra and Gause a plethora of mathematical models have been put forward to explain certain temporal population patterns, real or fancied, perceived in nature. Even the earliest models recognized that few species exist in isolation; cognizance must be taken not only of their interactions with the abiotic environment, but also with their cohabitants in the ecosystem. With few exceptions models of interacting populations have been at the overall population level, couched in terms of time invariant ordinary differential or difference equations. However, populations are intrinsically distributed parameter systems. Total population numbers are not accurate indicators of their dynamic state unless the populations have achieved a stable age distribution and one can safely ignore other physiological indices such as size, mass, chemical composition, etc. Even in the simple ecosystem of a bacterial chemostat, lumped-parameter models have had to be abandoned in favor of more detailed functional equations (Frederickson et al. 1967, Williams 1971).

A second ubiquitous feature of natural populations that has not received the attention it deserves in quantitative ecological theory is the recognition that few populations live in a constant environment; both seasonal and daily cycles militate against a pure and continuing Malthusian growth (Skellam 1967, Fretwell 1972, Nicholson 1957).

On several counts, therefore, one is led to suspect that finite-dimensional autonomous equations are generally not viable models on which to base ecological theory. To relax either the assumption of a stable age distribution or a constant environment is to alter dramatically, even reverse, the quantitative and qualitative consequences of the model as they pertain to actual populations. Indeed, one can easily construct examples of time-varying linear systems, $\dot{x} = A(t)x$, whose eigenvalues are stationary in the left half plane, yet the system is unstable. In general, little can be said about the properties of time-varying systems by examining their time-invariant counterpart (Desoer 1969).

Nevertheless, the theoretical ecologist must seek some reduced description of the biosphere, to perceive order in complexity through a few comprehensible collective properties. There is certainly no guarantee that this search will not be in vain. Perhaps, as some say of the human brain, an ecosystem is its own minimal representation and all we can hope for is a one-for-one computer simulation. If true, this would indeed be discouraging. So, we complicate our models step by step, hoping that before we pass into the abyss of mathematical intractability, a reasonable compromise will have been struck between precision and generality.

At each step in this process, the emphasis must be placed on qualitative rather than quantitative conclusions. This is not to avoid analytical or numerical difficulty but rather an explicit recognition that (i) until there is a quantum jump in instrumentation and measurement techniques, ecological data will remain meager and mostly descriptive; (ii) even given an ideal "population meter," we are likely to
find that ecological systems are not as tightly stabilized as those we encounter in engineering or physiology. Rather, they seem to be more loosely organized, endowed with great plasticity in adapting to environmental variations and coupled not by the rigid laws of chemistry and physics but by the flexible behavior patterns of their constituent populations. Therefore, Levins (1966) and others have stressed the desirability of seeking conclusions that are insensitive to the detailed assumptions or parameter values of the model and developing alternative but overlapping models whose intersecting conclusions may be the best we can hope for as general principles.

Fortunately, in recent years reasonable agreement has coalesced concerning the equations that govern the aging of biological populations (Von Foerster 1959, Trucco 1965, Oldfield 1966, Frederickson et al., 1967, Sinko and Streiffer 1967, Langhaa 1972). It behooves us, therefore, in imitation of physics, to investigate all of the mathematical, i.e. logical, consequences of these demographic equations, keeping one eye on the experimental data yet unexplained.

We shall examine the dynamic effects of age structure and environmental periodicity on the behavior of interacting populations. Our theme is that certain novel phenomena emerge as a natural consequence of viewing the population as a distributed parameter system with periodic forcing. In particular, we can expect periodic behavior whose origin is quite different from that classically associated with population oscillations modeled by lumped-parameter models (May 1972). In addition, an interesting phenomenon, that of “distributed resonances”—analogous to harmonic beats in linear systems—emerges as a candidate to explain certain long-term periodicities and population outbreaks observed in laboratory ecosystems and in nature.

It is important to note that our analysis is limited to the linearized version of the equations; thus all we can hope for is to demonstrate the instabilities that lead to the periodic solutions and an estimate of their frequency. Simulation studies of these models will be presented elsewhere (Auslander et al. 1974). However, the qualitative conclusions are fairly robust corollaries of a quite general model. Since these models are part of a larger biological control study in progress, we have couched our language in terms of insect parasite-host systems. The results are easily generalizable to other types of population interactions.

In order to avoid extensive mathematical detours which tend to obscure the arguments we have collected most of the computations in the appendices.

**The Population Balance Model in a Periodic Environment**

The equations describing the population density function have been derived in several contexts (Hurlburt and Katz 1964, Von Foerster 1959, Sinko and Streiffer 1967, Frederickson et al., 1967, Oldfield 1966). First, consider a spatially homogeneous population. We assume that the state of a particular individual in a population at time \( t \) is specified by the chronological age since birth, \( a \), and a set of physiological parameters \( \xi = (\xi_1, \ldots, \xi_k) \). These may include size, mass, chemical compositions, or any other quantities having a bearing on the individual’s rate of growth or reproduction. Therefore, an individual is represented by a point \( (t, a, \xi) \) in \( \mathbb{R}^{n+2} \) and, as usual, we assume that knowledge of the state \( (t, a, \xi) \) is sufficient to predict the trajectory of the individual according to the vector field:

\[
\frac{da}{dt} = 1, \quad \frac{d\xi}{dt} = \frac{d\xi}{da} = g(t, a, \xi),
\]

where \( g(\cdot) \) is the growth rate for the quantities \( \xi(t) \). A population of such individuals can be described by defining a set of density functions \( n_k(t, a, \xi) \) on the state space, one for each population. The equations of motion for the population densities are obtained by applying a conservation law to each population \( n_k \):

\[
\frac{\partial n_k}{\partial t} + \frac{\partial n_k}{\partial a} + \sum_{i=1}^{N} \frac{\partial}{\partial \xi_i} (g_{ik} n_k) = -\mu_k n_k,
\]

where \( \mu_k(\cdot) \) is a functional giving the death rate for population \( k \).

The initial distributions \( n_k(0, a, \xi) \), for equations (2) are presumed known. The unique character of the demographic equations is embodied in the death rate functional and in the boundary conditions that specify the sink and source terms for individuals. In particular, the boundary condition specifies the rate of entry of new individuals into the population at age zero as a functional of the adult breeding population. This is an integral feedback that typically takes the form

\[
n_k(t, 0, \xi) = \int \int b_k(t, a, \xi, \xi') n_k(t, a, \xi') \ da \, d\xi',
\]

where \( b_k(\cdot) \) is the “maternity function” weighting the contribution of the adult stock to the neonates. The character of any population, insofar as its numerical abundance is concerned, is completely de-

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3 Note that for constant growth rates, \( g_{ik} = \text{constant} \), and zero mortality rate, \( \mu_k = 0 \), equation (2) reduces to the Liouville Equation from statistical mechanics. In general, however, we will not be able to use the method of Gibb's Ensembles as employed by Kerner (1972) to obtain a reduced description of biological populations.
We can illustrate the population system schematically as shown in Fig. 1 by taking an instantaneous snapshot of the age profile at \( t = \text{constant} \) (Appendix I). From Fig. 1 we can see that equations (4) describe a distributed-parameter positive-feedback system. To illustrate this, in Appendix II, equations (4) are cast in conventional feedback (block-diagram) form. Engineering systems of this type are notoriously unstable if the parameters are not kept within well defined limits. For our purposes, however, we shall employ heuristic diagrams such as Fig. 1, which do not require the system to be linear.

The usual procedure for solving equations (4) then is to first obtain the general solution to (4a), which can be written (Appendix III):

\[
n(t, a) = n(t-a, 0) \sigma(t, a), \tag{5a}
\]

where \( \sigma(t, a) \) is the probability that an individual born \( (t-a) \) time units ago will survive to time \( t \). (The solution is given explicitly in Appendix III). Substituting (5a) in the boundary condition, equation (4b), one obtains an integral equation

\[
n(t, 0) = \int_0^t b(t, a') \sigma(t, a') n(t-a', 0) \, da'. \tag{5b}
\]

This equation must be solved for the birthrate, \( n(t, 0) \), then resubstituted in (5a) to obtain \( n(t, a) \). (Langhaar 1972).

Since we are interested in the effects of periodic forcing on the system, we shall proceed differently. Let us assume that the equilibrium age-distribution density function, \( n(a) \), is time invariant, so that

\[
n(a) = n(0)e^{-\alpha a} \]

will satisfy both equations (4a) and (4b). An equilibrium age distribution may never be actually achieved by a given population, but it is a convenient state to use as a reference from which to measure deviations. The boundary condition (4b) at equilibrium must satisfy

\[
n(0) = \int b(a)n(a)\, da, \tag{6}
\]

i.e.,

\[
1 = \int b(a)e^{-\alpha a}\, da,
\]

where \( b(a) \) is the steady state birthrate.

Next, we linearize about the equilibrium distribution, \( n(a) \), by introducing a normalized perturbation in the population distribution

\[
\chi(t, a) = \frac{n(t, a) - n(a)}{n(0)},
\]

and the death rate

\[
\Delta \mu(t) = \mu(t) - \bar{\mu}.
\]

Substituting in equation (4a) and neglecting all but first order terms, we obtain the linearized system

\[
\frac{\partial \chi(t, a)}{\partial t} + \frac{\partial \chi(t, a)}{\partial a} = -\bar{\mu} \chi(t, a) + n(a)u_2(t), \tag{7a}
\]

for the insect species it is convenient to use a time and age scale measured in "degree-days" since physiological development rates are frequently linear in temperature above a certain threshold (Hughes 1962, Gilbert and Gutierrez 1973).
where \( u_2(t) = -\Delta \mu(t) / n(0) \) is a (normalized) periodic perturbation in the death rate due to external forcing.

Similarly, the boundary condition (4b) is linearized about the equilibrium birth rate, by introducing perturbations: \( \Delta b(t, a) = b(t, a) - b(a) \) to obtain

\[
x(t, 0) = \int_a^x b(a) x(t, a) \, da + u_1(t),
\]

(7b)

where \( u_1(t) = \int_a^x \Delta b(t, a)[n(a)/n(0)] \, da \) is the periodic input to the birth rate (Fig. 1).

For the moment, let us assume that all reproduction occurs at a single age, \( a = \alpha \), i.e., \( b(t, a) = b(t) \cdot \delta(t - \alpha) \). Then, using (6), the linearized birth rate, (7b), becomes

\[
x(t, 0) = e^{\hat{b}a} x(t, a) + u_1(t).
\]

(7c)

The input-output behavior of the system is best studied by taking the Laplace transform of equations (7a) and (7c):

\[
dX(s, a)/da = -(s + \hat{\mu}) X(s, a) + e^{-\hat{b}a} U_2(s)
\]

and

\[
X(s, 0) = e^{\hat{b}a} X(s, a) + U_1(s),
\]

where \( X(s, a) = Lx(t, a), \quad U_i(s) = Lu_i(s), \quad i = 1, 2 \). The solution to this set is

\[
X(s, a) = \frac{e^{-(s+\hat{\mu})a}}{1 - e^{-\hat{b}a}} U_1(s) + \frac{e^{-\hat{b}a}}{s} U_2(s).
\]

(8)

The total-population deviation from the stable age distribution is

\[
Y(s) = \int_a^x X(s, a) \, da,
\]

\[
= \frac{1}{s + \hat{\mu} + \frac{1}{\hat{\mu} + \hat{\beta}} U_1(s) + \frac{1}{\hat{\mu} + \hat{\beta}} U_2(s).
\]

(9)

The frequency response to the birth rate forcing is given by the transfer function

\[
G(i\omega) = Y(i\omega)/U_1(i\omega),
\]

(10)

which exhibits resonances at \( \alpha/\tau = n, \quad n = 1, 2, \ldots \), where \( \tau = 2\pi/\omega \) is the period of the forcing signal. This result is exactly what one would expect when the periodic effect on birth rate is exactly in phase with the aging delay.

The magnitudes of the resonance peaks exhibited by the point birth model are infinite. However, let us replace the birth function by an average birthrate, \( \bar{b} \), over a finite “breeding window” \((\alpha, \alpha + \gamma)\), Fig. 2, so that equation (6) becomes

\[
n(0) = \bar{b} \int_a^{\alpha + \gamma} e^{-\hat{b}a} n(0) \, da
\]

or

\[
\bar{b} = \frac{\hat{\mu}}{e^{-\hat{b}a}(1 - e^{-\hat{b}\gamma})}.
\]

(11)

Fig. 2. Average fecundity schedule in the “breeding window” \((\alpha, \alpha + \gamma)\).

Using this mean birthrate and solving the Laplace transform equations as before, we obtain

\[
Y(s) = \frac{1}{s + \hat{\mu} + \hat{\beta}} \left( \frac{e^{-\hat{b}a} (1 - e^{-(\hat{\mu} + \hat{\beta})\gamma})}{1 - e^{-\hat{b}\gamma}} \right) U_1(s) + \frac{U_2(s)}{\hat{\mu} + \hat{\beta}}.
\]

(12)

The resonances at the poles of \( G_1(s) \) now are finite; but, as above, they can also occur with periods much longer than the generation time of the forcing period.

Note that in both cases, because the death rate is not age specific, this periodic forcing does not excite a resonance in the population profile.

In general, we can see that any periodic influence in the birth and death rates that acts in an age-specific fashion (i.e., unequally on all age classes) will excite waves in the population age profile. These waves propagate through the age structure until they reach the breeding window \((\alpha, \alpha + \gamma)\), whence the positive birth feedback reexcites a secondary wave at \( a = 0 \). If these waves are excited at a frequency approximately proportional to a generation time, \((\alpha + \gamma)/2\), constructive (or destructive) reinforcement will occur tending to produce a dramatic periodicity in the overall population numbers.

A third source of periodic excitation is in the differential effects of temperature and other abiotic factors on maturation rates. If, instead of chronological age, we employ a more meaningful physiological measure such as size, mass, or chemical concentrations, then equation (4a) takes the form

\[
\frac{\partial n}{\partial t} + \partial (gn)/\partial \xi = -\mu n,
\]

(13)

where \( g = g[T(t), \xi, n] \). Since growth rate is generally age specific, periodic temperature variations \( T(t) \) can excite traveling waves in the population profile that can interact with those generated by the birth and death terms.

It is apparent from this discussion that the crucial time scales involved are the generation times of the species vs. the forcing frequency. Therefore, one can distinguish three types of populations with regard to their response to periodic inputs: (1)
many generations per cycle, (2) approximately one generation per cycle, and (3) many cycles per generation.

In the following models we have in mind daily and seasonal effects on fecundity schedules, especially of insect populations, thereby restricting our attention principally to cases (1) and (3). However, the analysis is readily applicable to arbitrary forcing signals.

One must proceed with caution, however, in adopting models to describe particular species in their natural setting; the idiosyncrasies of each species must be properly taken into account. For example, in insects exhibiting diapause and/or voluntunism, developmental age (measured, say, in degree-days (Hughes 1962)) is essentially arrested, producing a horizontal characteristic noted in Appendix II. These segments may simply be sectioned out, and the population growth continued the following season by including a factor to account for overwintering mortality. For many insect populations, the system is started anew each year; the only "memory" of the preceding year's age structure is contained in the magnitude and perhaps the hatching schedule of the first egg "batch" the following year. (Clearly, such populations are not likely to approach a stable age distribution unless there are many overlapping generations in one season.)

There is, as yet, scanty field data to support or refute mathematical models such as we present here. However, the qualitative conclusions are in accord with observations on natural populations. A detailed study of a laboratory ecosystem amenable to quantitative analysis by these methods will be presented in a subsequent publication (Auslander et al. 1974).

In the following section we present the results of some simplified analyses which will give us some feeling for the distributed resonance phenomenon. Although the complexity of the equations ultimately forces us to computer simulation, the qualitative effects can be studied by linear analysis and an estimate of the resonance frequency obtained.

**Coupled Systems**

Fig. 3–5 represent distributed parameter systems with distributed and boundary couplings (Takahashi et al. 1970). Such systems are considerably more difficult to analyze than the finite dimensional coupled systems usually employed in population modeling. In the following we shall examine a sequence of approximate two-species models, and derive input-output relations in the frequency domain. We shall adopt the notational convention of using subscripts \( p \) (predator, parasite, etc.) and \( h \) herbivore, host, etc.) to denote the interacting species.

**Predator-prey system: point birth and death rates controlled by total population numbers.**

In equation (9) we replace the term for intrinsic death rate for each species by a mortality factor that depends on the total population of the other species (Fig. 3). The total population of the predator, \( Y_p(s) \) in the frequency domain, is therefore given by

\[
Y_p(s) = \frac{1}{s + \rho_p} \frac{1}{1 - e^{-\rho_{sp}}} U_p(s) + \frac{\rho_{ph}}{\rho_{ph}} Y_h(s),
\]

where \( U_p(s) \) is the environmental input to the birth-rate of the predator. Therefore, the total population of the prey, \( Y_h(s) \), is given by

\[
Y_h(s) = \frac{1}{s + \rho_h} \frac{1}{1 - e^{-\rho_{sh}}} U_h(s) - \frac{\rho_{hp}}{\rho_{hp}} Y_p(s).
\]

As in equation (9), point birth is assumed for both of the species. The two equations may be solved for \( Y_p(s) \) and \( Y_h(s) \):

\[
\begin{bmatrix}
Y_p(s) \\
Y_h(s)
\end{bmatrix} = \frac{s^2}{s^2 + \Omega^2} \times
\begin{bmatrix}
\frac{1}{s + \rho_p} \frac{1}{1 - e^{-\rho_{sp}}} & \frac{1}{\rho_{ph}} \frac{1}{s + \rho_h} \\
\frac{1}{\rho_{hp}} & \frac{1}{s + \rho_h} \frac{1}{1 - e^{-\rho_{sh}}}
\end{bmatrix}
\begin{bmatrix}
U_p(s) \\
U_h(s)
\end{bmatrix},
\]

where

\[
\Omega^2 = \frac{\rho_{ph} \rho_{hp}}{\rho_{ph} \rho_{hp}}.
\]

In addition to the resonance terms \( (1 - e^{-\rho_{sp}}) \) and \( (1 - e^{-\rho_{sh}}) \) which we saw in equation (9), the (linearized) total-population response is characterized by harmonic oscillation terms \( (s^2 + \Omega^2) \) of frequency \( \Omega \). (Compare Volterra-Lotka predator-prey frequency (Pielou 1969): \( \Omega = [(\text{prey birth rate}) \times (\text{predator death rate})]^\frac{1}{2} \). Consequently, the response of each
population will involve at least two sinusoids of differing frequencies leading to a new phenomenon: harmonic “beats” at a frequency proportional to the difference between the interaction frequency and the birthrate resonance frequencies (Towne 1967: 212, Crawford 1968: 28).

The population is thus analogous to a dispersive medium through which sets of harmonic waves propagate. These waves will interfere, constructively and/or destructively, to produce periodic variations in the population levels. The important feature of these beat resonances is that they may also recur on a time scale much longer than either the external forcing frequency or the lifespan of an individual in the population (i.e. the beat period for two different frequencies $\Omega_1$ and $\Omega_2$ is $2\pi/(\Omega_1 - \Omega_2)$).

A detailed analysis of the beat phenomena would not be useful in view of the unrealistic approximations made in this model. However, as we shall discuss later the qualitative phenomena predicted by this simple model are characteristic of all coupled-population systems.

**Host-parasite system: point birth, parasitization in egg stage**

This is a special case of host-parasite coupling where a fraction, $\Delta h(t)$, is parasitized out of the total host population at age zero, $h_e(t)$ (Fig. 4). We shall assume that the probability of parasitization is analogous to a Poisson process and employ a variant of the usual Nicholson-Bailey form (Hassell and Varley 1967):

$$\Delta h(t) = h_e(t) (1 - e^{-Ap_e(\alpha_p, t)})$$

where $A$ is the parasite search area, $p(\alpha_p, t)$ is the parasite population at its single reproductive age, $\alpha_p$, and $\kappa$ is a correction exponent for nonrandom search capacity. In this approximation the model is similar to the classical Nicholson-Bailey model (Smith 1968).

Since, from Fig. 4 $h_0(t) = h_e(t) - \Delta h(t)$ is the host population at age zero, the number of hosts eligible for parasitization is given by

$$h_e(t) = b_h(\alpha_h, t) [h_e(t - \alpha_h) - \Delta h(t - \alpha_h)]$$

where $b_h$ is birthrate of the host for single point birth at age $\alpha_h$ and $\alpha_h$ is the survivorship function for the host (equation (5) and Appendix III).

If the population of the parasitized host, $\Delta h(t)$, is exactly equal to the population of the parasite at age zero, the parasite population at its single point reproductive age, $\alpha_p$, is:

$$P(\alpha_p, t) = \sigma_p(t - \alpha_p, t) \Delta h(t - \alpha_p)$$

where $\sigma_p$ is the survivorship function of the parasite.

As before, equations (14) through (16) may be linearized about an equilibrium state (Appendix IV) to yield a set of coupled time-difference equations for the deviations $x_h(t)$ and $x_p(t)$ of $h_e$ and $\Delta h$:

$$x_h(t) = c_1\{x_h(t - \alpha_h) - x_p(t - \alpha_p)\} + c_0u(t),$$

$$x_p(t) = c_2x_p(t - \alpha_p) + c_3x_h(t),$$

where $u(t)$ is the periodic input on the birthrate of the host and $c_0$, $c_1$, $c_2$ & $c_3$ are linearization constants. The characteristic equation of the coupled system is

$$(1 - c_1e^{-\alpha_h}) (1 - c_2e^{-\alpha_p}) + c_1c_3e^{-\alpha_h} = 0.$$  

An investigation of the roots (eigenvalues) of this equation again reveals a set of oscillatory modes which may produce a “beat” when the birthrate forcing is periodic. (Appendix IV).

**General host-parasite system**

The preceding treatment may be generalized to couplings of the host and parasite populations where the birthrates and predation occur over finite age spans as shown in Fig. 5. The basic equations are:

$$\partial h(t, a) / \partial t + \partial \Delta h(t, a) / \partial a = -\mu h(t, a),$$

$$\partial p(t, a) / \partial t + \partial \Delta p(t, a) / \partial a = -\mu p(t, a).$$

Let us examine the birth and death rate functionals for this system. The death rate of the host population should depend on age, $a$; time in the season, $t$; the number of hosts present per unit area (i.e., density control),

$$\int_0^a h(t, a) da = H(t);$$

the number of parasite adults eligible to attack the host,

$$\int_0^a p(t, a) p(t, a) da = P(t);$$

and the number of hosts eligible for parasitism,
interactions. However, we shall avoid these behavioral intricacies and continue to employ the Nicholson-Bailey form (c.f. equation (14)):

\[ p(t,a) \sim H_0(1 - e^{-\Delta t}) \]

A number of other functional response models could have as easily been used, e.g., Holling (1959, 1965, 1966), Huffaker et al. (1971).

Now, the birth and death rates of both parasite and host are subject to periodic influences, \( u(t) \). This is introduced, for instance, into the birthrate of the host, \( b_h \), in the form:

\[ b_h = u(t) \cdot f_h(a, H, H) \]

The periodic functions acting on \( b_g, \mu_h \) and \( \mu_p \) share the same frequency, but are possibly in different phases if the daily or seasonal cycle affects birth and death of each species differently.

**Host-parasite system: interactions over finite age intervals**

Here we simplify the preceding model by letting the age-specific factors be unity in the respective age intervals. Let \( x_p(t) \) and \( x_h(t) \) be the population deviations from the equilibrium distributions as before and denote the reproductive and parasitized segments of the population as (Fig. 5):

\[ H_h(t) = \int_{\phi_1}^{\phi_2} x_h(t, a) \, da, \]
\[ H_t(t) = \int_{\phi_1}^{\phi_2} x_t(t, a) \, da, \]
\[ P(t) = \int_{\phi_1}^{\phi_2} x_p(t, a) \, da. \]

The linearized equations for the parasite are:

\[ \frac{dx_p(t, a)}{dt} + \frac{dx_p(t, a)}{da} = -\mu_p x_p(t, a), \]
\[ x_p(t, 0) = C_1 P + C_2 H_0, \]

where the coefficients \( C_1 \) and \( C_2 \) in (23) are determined by linearizing the search algorithm, equation (20).

The Laplace-transformed system is

\[ dX_p(s, a)/da = -(s + \mu_p) X(s, a), \]
\[ X_p(s, 0) = C_1 P(s) + C_2 H_0(s), \]

where \( P(s) = \mathcal{L}(P(t)) \) and \( H_0(s) = \mathcal{L}(H_0(t)) \). The solution is:

\[ X_p(s, a) = e^{-(s+\mu_p)a}[C_1 P(s) + C_2 H_0(s)]. \]

Consequently,

\[ P(s) = G_1(s) H_0(s), \]

which, when solved for \( P(s) \) can be written

\[ P(s) = G_1(s) H_0(s), \]

where \( G_1(s) \) is a known function of \( s \) (see Appendix V). The total deviation of the parasite popula-
tion from the equilibrium distribution may also be computed as
\[ Y_p(s) = \int_0^s X_p(s, a) \, da = G_2(s)H_0(s), \] (28)
where
\[ G_2(s) = \frac{C_1G_1(s) + C_2}{s + \bar{\mu}_p}. \]

The linearized, transformed equations for the host population are
\[ dX_h(s, a)/da = -(s + \bar{\mu}_h)X_h(s, a) - \nu(a)P(s), \] (29)
\[ X_h(s, 0) = C_0H(s) + kU(s), \] (30)
where \( C_0 \) and \( k \) are linearization constants and \( U(s) = Lu(t) \) is the periodic input which we assume to affect only the host birthrate, the parasite having adapted its life cycle to that of the host. For simplicity let us assume that parasitization occurs at a constant rate, \( \nu \), only in the age interval \( (a_0, a_0 + \gamma_0) \), so that \( \nu(a) \) in equation (29) will be the step function:
\[ \nu = \begin{cases} \nu & \text{for } a_0 \leq a \leq a_0 + \gamma_0 \\ 0 & \text{otherwise} \end{cases} \] (31)

These equations may be solved sequentially in the three age groups, \((0, a_0), (a_0, a_0 + \gamma_0), (a_0 + \gamma_0, \infty)\) and the quantities \( H_0(s), H(s), \) and \( Y_h(s) = \int_0^s X(s, a) \, da \) evaluated. The resulting relations take the following form:
\[ H_0(s) = G_0(s)H(s) + G_1(s)P(s) + G_5(s)U(s), \] (32)
\[ H(s) = G_0(s)P(s) + G_1(s)U(s), \] (33)
\[ Y_h(s) = G_0(s)H(s) + G_9(s)P(s) + G_{10}(s)U(s), \] (34)
where \( G_i(s), i = 3, \ldots, 10, \) are complicated functions of \( s \), in particular, of the delay operator, \( e^{-st} \).

It may be helpful to visualize the system interactions (i.e. equations (27), (28), (32), (33) and (34)) with the signal flow graph shown in Fig. 6 (Takahashi et al., 1970).

It is possible to solve the five equations for the five unknowns, the solutions taking the following general form:
\[ H_0(s) = K_0(s)U(s), \]
\[ H(s) = K_h(s)U(s), \]
\[ P(s) = K_p(s)U(s) \] (35a)
and
\[ Y_h(s) = G_p(s)U(s), \]
\[ Y_h(s) = G_h(s)U(s). \] (35b)

The resulting transfer functions, \( K_0(s), K_h(s), K_p(s), G_p(s) \) and \( G_h(s) \) are irrational due to the various age delays in the system. The roots (eigenvalues) of this system can not be computed analytically without further simplifying assumptions. However, a glance at equations (27), (28), (32), (33), (34), and Fig. 6 shows that the qualitative behavior of the total populations \((Y_h(s) \) and \( Y_p(s)\)) will involve the following three effects: (a) the harmonic birthrate excitation, \( U(s) \), will generate waves in the host age profile that will resonate as discussed previously, (b) the resulting periodicity in \( H_0(t) \) will excite waves in the parasite age profile that, in turn, will feed back on the host population with a delay, setting up secondary waves in the host age profile, and (c) the complex spectrum excited by \( U(s) \) and the age-specific interaction will periodically produce a beat resonance in each population as signals reverberate within the network, Fig. 6, containing delays.
We note in passing that intraspecific competition may produce the same effects noted above. For instance, inter-age-class competition in effect partitions the population into two competing subpopulations (Slobodkin 1954, 1961, e.g., adult males driving out subadult males). This can be modeled by introducing an age- and density-dependent mortality, as shown in Fig. 7, where the death rate for a young age class, $\mu_2$, is an increasing function of the adult stock, $N$.

**Herbivore-resource system**

The last example is a coupled system consisting of a herbivore, $h(t, a)$, feeding on a plant resource, $R(t)$, whose abundance affects the host birthrate as shown in Fig. 8. In the absence of herbivores, we shall assume that the resource grows logistically and that the periodic input, $u(t)$, acts only on the plants, so that we are dealing here with a hybrid lumped-distributed dynamical system of the form:

$$\frac{dR(t)}{dt} = f(R, h, u), \quad (36a)$$

$$\frac{dh(t, a)}{dt} + \frac{\partial h(t, a)}{\partial a} = -\mu h(t, a), \quad (36b)$$

$$h(t, 0) = \int_a^{\omega} b(a, R) h(t, a) \, da. \quad (36c)$$

Reasonable nonlinear interaction functions for the two systems are proposed in Appendix VI. In the following we shall concern ourselves only with the linear analysis.

The linearized system is described in terms of deviations of the herbivore, $x(t, a)$, and the resource, $r(t)$, both measured from an equilibrium state. The dynamic equation for the plant is

$$\frac{dr(t)}{dt} = -Ar(t) - Br(t) + Cu(t), \quad (37)$$

where $A$, $B$, and $C$ are coefficients determined by linearization, and $y(t)$ is the total population deviation of the herbivore, i.e.,

$$y(t) = \int_a^{\omega} x(t, a) \, da. \quad (38)$$

For the herbivore we have

$$\frac{\partial x(t, a)}{\partial t} + \frac{\partial x(t, a)}{\partial a} = -\mu x(t, a) \quad (39)$$

and

$$x(t, 0) = g(t) + b \int_a^{\omega} x(t, a) \, da, \quad (40)$$

where $g$ is a constant, and the birthrate is assumed to be constant over an age interval $(\alpha, \alpha + \gamma)$.

Solving equations (39) and (40) in the Laplace domain as before, we obtain

$$X(s, a) = e^{-\alpha \gamma} s G(s) R(s), \quad (41)$$

where $R(s) = Lr(t)$ and

$$G(s) = \frac{g}{1 - \frac{b}{s + \mu} \left( e^{-\alpha \gamma} s - e^{-\alpha \gamma (s + \gamma)} \right)}. \quad (42)$$

From equations (38) and (41), we find the total population in the Laplace domain:

$$Y(s) = \left[ 1/(s + \mu) \right] G(s) R(s). \quad (43)$$

Inserting the last expression into equation (37), the resource equation is

$$R(s) = \frac{C}{s + A + [B/(s + \mu)]} G(s) U(s). \quad (44)$$

The characteristic equation of the system is given by the denominator of equation (44) as

$$s + A + [B/(s + \mu)] G(s) = 0. \quad (45)$$

In order to get a better feeling for the system dynamics, let us once again make the point birth assumption, $b(a) = b^* \delta(a - a)$. Then $G(s)$ simplifies to

$$G^* (s) = \frac{g}{1 - b^* e^{-\alpha \gamma}}. \quad (46)$$

so that the characteristic equation becomes

$$1 + \frac{B g}{(s + A)(s + \mu)(1 - b^* e^{-\alpha \gamma})} = 0. \quad (47)$$

Here the product $B \cdot g$ is a measure of: (effect of herbivore population on resource level) $\times$ (effect of resource on herbivore birthrate). Equation (47) has an infinite number of roots (system eigenvalues) for each value of $B \cdot g$.

As $B \cdot g$ varies between zero and infinity, each root traces a path on the complex plane; this root locus gives a good picture of the linearized system dynamics under various operating conditions (Takashi et al. 1970, Krall 1971). When $B \cdot g = 0$, equation (47) will reduce to

$$(s + A)(s + \mu)(1 - b^* e^{-\alpha \gamma}) = 0.$$
Consequently the roots at $Bg = 0$ are located at

$$s = -A, \quad s = -\mu,$$

and those that will satisfy

$$e^{(s+\beta)a} = b^*.$$  \hspace{1cm} (48)

Equation (48) has one real root, $s = \rho$, such that

$$\rho + \mu < 0 \quad \text{if} \quad b^* < 1,$$

$$\rho + \mu > 0 \quad \text{if} \quad b^* > 1.$$  \hspace{1cm} (49)

The complex roots of (48) are investigated by setting

$$s = \sigma + i\omega$$

and equating real and imaginary parts of equation (48). The roots are at $\sigma = \rho$ and $\omega = 2n\pi/\alpha$, $n = 1, 2, \ldots$.

As $Bg$ increases towards infinity the roots approach the asymptotes at $\omega = \pm 2n\pi/\alpha$, $n = 0, 1, 2, \ldots$. The general pattern of the root locus is sketched in Fig. 9, where it is assumed that $b^* > 1$. The arrows indicate direction of increasing $B \cdot g$. The branches start at $Bg = 0$ (denoted by "x") and proceed to $Bg = +\text{(infty)}$ (denoted by "o"). The roots of equation (47) for a prescribed value of $Bg$ are found on the branches, for instance, as denoted by $P_1$, $P'_1$, $P_2$, $P_3$, $P'_3$, and so on.

Knowing the root distribution for equation (45), the frequency response for the resource, $R(i\omega)/U(i\omega)$, and the total population, $Y(i\omega)/U(i\omega)$, can be obtained from equations (44) and (43). Since the first pair of the conjugate complex roots ($P_1$ and $P'_1$ in Fig. 8) could be very close to the real axis, the resulting resonance frequency could be arbitrarily long.

If the herbivore reproductive window has a finite width, $\gamma$, equation (46) must be replaced by equa-

The first and second roots, $s = -A$ and $-\mu$, remain unchanged. Since investigation of the complex set of roots is considerably more complicated than that of Fig. 8, it will not be presented here. Here, however, an interesting new feature emerges that is perhaps of some biological significance. The root locus appears to be extremely sensitive to variations in the breeding window width, $\gamma$. When $\gamma$ becomes greater than $\alpha$, there occurs a sudden jump (or "bifurcation") in root locations in the complex plane, indicating a qualitative change in dynamic behavior.

This is interesting from the following point of view. As mentioned earlier, insect development rates are generally temperature dependent. If age is measured in degree-days (Hughes 1962), it is clear that the size of the breeding window, $\gamma$, is influenced by weather to a great extent. A favorable sequence of weather events, such as early spring and optimum moisture conditions, could increase $\gamma$ past the bifurcation point, and excite a population resonance which, depending on the number of generations per season, may produce an outbreak in succeeding years. That a sequence of favorable weather events can trigger a pest outbreak is well known in entomology (e.g., Watt 1968: 149–152); we conjecture that the above mechanism is an important factor in such outbreaks. Although the qualitative possibility of such an effect is inherent in the model, we can not answer at this stage whether the parameter values required to produce it characterize any real system. A detailed discussion implicating climatic factors as triggers for population outbreaks is given in Watt (1968), Section 6.2.

Investigating the stability properties of the general nonlinear population model in a periodic environment is a delicate task, since few techniques exist even for linear distributed systems with variable coefficients. Even at the overall population level, the introduction of periodic parameters dramatically alters the stability properties. For example, if equations (4) are integrated over all ages

$$dN(t)/dt = \int_a^s b(t) n(t) da - \int_a^s y(t) n(t) da,$$

where

$$N(t) = \int_a^s n(t, a) da.$$

Assuming that the maternity and mortality coefficients are linear functions of $N_1$ and $N_2$ we obtain the Gause competition equations. However, if the coefficients are periodic functions, simulation experiments indicate that it is possible to completely reverse the outcome of a given competitive experiment according to the frequency and amplitude of
the parameters. This is not surprising in view of the comments on linear time-varying systems made earlier.

**Effects Tending to Obliterate the Population Oscillations**

Two important aspects of biological populations are not described by the population balance equations (2).

First, although we have employed chronological age as our measure of growth rate, it is almost always preferable to use a physiological time scale (e.g., degree-days) when dealing with actual populations (Hughes 1962, Gilbert & Gutierrez 1973, Barr et al. 1972). Due to various effects including genetic diversity, a population can not be expected to age synchronously on such a scale. To account for the dispersion in growth rates, equation (1) must be modified to

$$\frac{\partial n_k}{\partial t} + \frac{\partial n_k}{\partial a} + \sum_i \frac{\partial}{\partial \xi_i}(g_{ik} n_k) + \sum_i \frac{\partial^2}{\partial \xi_i^2} (\sigma_{ik} n_k)$$

$$= -p_k n_k,$$

where $g_{ik}(t, a, \xi_i, n)$ is now the mean growth rate and $\sigma_{ik}(t, a, \xi_i, n)$ is the dispersion coefficient. Equation (50), which bears an obvious resemblance to the forward Kolmogorov equation (Weiss 1968), is no longer hyperbolic. The effect of the parabolic dispersion term is to reduce the resonance and ultimately destroy it if $\sigma/g$ is not sufficiently small.

Second, we have not included any spatial coordinate in our equations, an omission tantamount to assuming that migration occurs continuously and at a rate sufficiently faster than the demographic time scale that the population may be considered spatially uniform. This is patently false in most cases, especially for insect populations, where spatial inhomogeneity and density-dependent migrations play a dominant stabilizing role (Huffaker and Stinner 1971, Calhoun and Webb 1953, Birch 1970). There are several ways to account for migration effects—for example, by adding a spatial convective term $\vec{V} \cdot \nabla n$, where $\vec{V}$ is a mean migration vector. Or, if movements are rapid and random away from population centers, a spatial diffusion term, $D \nabla^2 n$, may suffice. (A general formulation of spatial effects is found in Rottenberg 1972). Clearly, any sort of density-dependent immigration will tend to obscure the resonances discussed above. Here the critical parameter would be $g/D$, the ratio of growth to spatial-dispersion rate. The resonance phenomenon occurring in a local population will be immediately translated into a spatial epizootic which propagates away from the center, reducing or obliterating completely the local outbreak (Watt 1968:149). Whether or not these beat- or resonance-induced immigrations can account for epizootics observed in nature will depend on the detailed nature of the processes involved; we shall defer this investigation to a later study.

We note in passing that the foregoing analysis is probably not relevant for human populations. The roots of equation (5b) have been computed from typical demographic data and yield a birthrate on the order of (Keyfitz 1972)

$$n(t, 0) \sim A e^{0.0075 t} + B e^{(-0.04 + 0.25 t)} t.$$  

The damping is such that, unless periodic reinforcement is provided, the age profile settles to its equilibrium distribution in approximately five generations (one generation ~ 26 years). However, human fecundity is affected primarily by economic and social factors whose time variations are hardly regular, so periodic reinforcement is unlikely.

Another, possibly crucial, factor in damping population waves would be a strongly density-dependent birthrate. A “trough” moving through the breeding window $(\alpha, \alpha + \gamma)$ would decrease crowding effects on the breeding population segment. The resulting increased fecundity would tend to restore the population to its equilibrium profile by a proportionally greater production of neonates. (In human populations this density response is called the Easterlin effect, but is an economic rather than biological phenomenon (Easterlin 1961)).

**The Reality of Long Term Population Periodicities**

The literature on periodic phenomena in populations is too extensive to be reviewed here; instead we confine ourselves to a few remarks in support of the theoretical models presented in Sections 2 and 3. Recent reviews of the subject can be found in Watt (1968), Odum (1971), Ricklefs (1973) and Emlen (1973).

Our investigations have been confined to one particular aspect of the problem of population cyclicity first suggested in a general way by Slobodkin (1954a, b) and Hutchison (1953, 1954): “Populations are feedback systems and . . . any such systems will of necessity act as a resonator, selectively responding to the fluctuations in the environment according to their time periodicity, the primary resonance being in the period of approximately one generation” (Slobodkin 1961:156).\(^8\)

\(^8\)The analogy between populations and physical resonators is not as close as Slobodkin would have it. In particular, selective frequency absorption does not occur in the same sense in population and energetic systems. While such analogies may be suggestive in a general way, they are unreliable since the details of the biological resonance effect are quite different from, say, a tuned RLC circuit.
Slobodkin cites some evidence of this effect in laboratory populations of Daphnia (Slobodkin 1961: 156, 1954b). Nicholson (1954, 1957) found that periodically varying the food supply in laboratory populations of the blowfly Lucilia cuprina Wied. resulted in periodic age-specific mortality and fecundity schedules. He observed a tendency for the population to entrain to a multiple of the forcing frequency, although the effect of frequency multiplications by nonlinear effects is pronounced. However, the envelope curve of the blowfly oscillation peaks suggests a longer period oscillation, apparently a manifestation of the beatlike phenomenon discussed earlier.

White and Huffaker (1969a, b) studied the effects of age-specific predation by Venturia canescens (Grav.) in laboratory populations of Anagasta kühniella (Zeller), and observed cycling on 4-, 8-, and 9-generation periods. These populations eventually condensed into near-discrete generations, an effect also predicted by the host-parasite-system model for finite age intervals and dealt with in another publication, Auslander et al. (1974). Hassell and Huffaker (1969) found that the parasite for this system, Venturia canescens (Grav.), behaved in approximately the manner assumed in the general host-parasite-system model.

There are numerous cases of purported long-term population cycles in nature, the most frequently cited being the Canadian furbearer populations, e.g., Butler (1953), Pitelka (1957). The evidence is not incontrovertible, however, since analogous cycles are seldom found in similar northern biomes. Cole (1954) and others have argued that sampling and smoothing techniques can manufacture illusory cycles out of random data.

Several fairly clear-cut examples of long term cycling can be found in insect populations, where variations over 4 or 5 orders of magnitude are frequently measured. In nature, however, the periodic forcing signal is rarely a pure sinusoid, and the measured frequency spectra are considerably more complex than those observed by Nicholson and Slobodkin in the laboratory. Baltensweiler (1964)

recorded outbreaks of larch budmoth, Zeiraphera griseana, at fairly regular 7–9-yr intervals, and Varley (1949) has observed similar, though less regular cycles in the pine moth, Bupalus. In both cases the outbreaks occurred with a wavelength much longer than either the generation time or any known meteorological cycle.

In at least one well-documented instance, a local outbreak triggered an epizootic in the fashion suggested earlier. (Belyea 1952, Watt 1968), although there is no evidence that the epicenter nucleated as we have suggested. Watt (1968) has also argued strongly in favor of meteorological effects as triggers for periodic outbreaks. The “dominant age-class” phenomenon has been observed in several fisheries and is believed to be triggered by some favorable environmental condition, followed perhaps by inter-age-class competition (Hjort 1926, Ricker 1950, Larkin 1971). The bifurcation phenomena, observed as the breeding window $\gamma$ is varied (c.f. Section 3.d), lend theoretical support for this argument.

Although it is possible that a plethora of entirely different mechanisms are operative for different taxonomic groups, one would like to believe that there are a small number of general ecological principles underlying all population periodicities. Nevertheless, a definitive explanation of population cycles must surely await more comprehensive demographic data on a variety of well-established examples.

SUMMARY AND CONCLUSIONS

We have argued that under fairly general conditions one can expect endogenous and exogenous limit-cycle behavior from interacting populations. The origin of these oscillations arises from wave propagation in the age profiles generated by age-specific interactions. These waves can coalesce into resonant beats, whose period may be much longer than either the exogenous or endogenous rhythms. Specifically, we have concerned ourselves with the following three phenomena: (1) Because daily or seasonal forcing enters the birth and death terms in an age-specific fashion, waves will be excited which will propagate through the population profile. Although the nonlinearities will produce frequency multiplications, it is clear that a periodic signal which is an approximate multiple of a generation time will produce a resonance as the maxima from the previous period are reinforced in each cycle. This phenomenon of “distributed resonance” has been observed in other distributed parameter systems. (2) Analogously, due to the age-specific nature of the population interactions, traveling waves will be excited in the host population, which will in turn feed back and excite similar waves in the para-
site-population profile. On an overall population scale, these will manifest themselves as an endogenous limit-cycle oscillation, though of an entirely different origin that the Volterra-Lotka type, it being the result of the distributed nature of the system.

(3) Each of these exogenous and endogenous periodic effects produces traveling waves through the population profile. These waves will interact to produce in the populations maxima and minima whose spacing may be much longer than either a seasonal cycle or a generation time. That is, a phenomenon analogous to beats in harmonic systems is to be expected, producing population outbreaks and crashes as the exogenous and endogenously excited waves reinforce and annihilate each other. We suggest that this last effect may contribute to certain long-term periodicities in natural populations.

Although we have argued mainly from the linearized analysis, the qualitative conclusions seem to be quite robust, dependent only on the general properties of the population-balance equations. The effects of growth dispersion due to genetic or environmental variability and the introduction of spatial effects (i.e., density-dependent migration) will tend to obliterate the resonance spectrum. However, in the latter case, one can expect that local population excursions will serve as migration nuclei, so that the temporal resonances will be translated into spatial epi-zoocitos.

It is certainly not our contention that all population systems inevitably exhibit periodic behavior due to the effects discussed above; ecology supports few such sweeping generalizations. However, all populations must obey the demographic equations (2), or their elaborations. Therefore, there is an inevitable tendency towards the type of behavior we have described, since the equations have the form of distributed positive-feedback systems. Our purpose here was to investigate the demographic equations by analyzing some simple models exhibiting the consequences of age-specific effects on numerical abundance.

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APPENDIX I

ANALOGUES FOR THE POPULATION EQUATIONS

The population balance equations are similar in many respects to other distributed parameter systems encountered in engineering, e.g., crystal growth (Randolf and Larson 1971, Hurhurt and Katz 1964), convective heat exchange (Takahashi et al. 1970, Friedly 1972, Himmell-blau and Bischoff 1968). It may be helpful for readers unfamiliar with such systems to visualize the aging process with the following mechanical analogue. The equations governing it are identical to the demographic equations (Keyfitz 1968).

The aging process is equivalent to a convective-flow process—for example, a conveyor belt (Fig. 10), moving at a velocity of one age unit per unit of time (distance along the belt is measured in age units). The instantaneous population-age profile can be viewed as a profile of “sand” deposited on the belt at the age-equals-zero boundary, representing the birthrate. The positive-birth rate feedback is shown in Fig. 10 as a controller which opens the birthrate “valve” according to the birth functional $\int b(a)n(t,a) da$. The mortality rate is simply leakage through the belt via perforations calibrated according to $\mu(t)$.

The equations governing this system are the equations of convective transport:

$$\frac{\partial n}{\partial t} + V \cdot \nabla n = -\mu n,$$

or

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu n,$$

since $V = 1$, $\nabla = \partial / \partial a$. Clearly, any convective system (e.g., fluid flow through a pipe, etc.) would serve equally well as an analogue. Couplings between these units are easily visualized as noted in the text. However, it is important to realize that the interaction schematized in Fig. 3 should not be interpreted as an energy pathway, although there is certainly an energetic transaction involved in order for the parasite to reproduce. While crucial at or above the community level of organization, energy is not the coin of the realm in population studies. This is not to say that thermodynamic considerations do not influence evolving behavior patterns so as to optimize caloric exchanges in some predator-prey relationships. But on the time scale of demographic changes, the determining factors in population interactions are the behavioral repertoires of the interacting
species. It is obvious that the searching predator or parasite is concerned primarily with visual, chemical, and other cues for success; energy considerations are mainly limiting factors (Watt 1968). The interaction in Fig. 3 should be viewed as a behavioral algorithm (or "functional response," Solomom 1949, Holling 1965, 1966) that must be decoded for each pair of interacting species being modeled. Of course, the behavioral algorithm may contain energy-related effects such as hunger state, etc. The principal thrust of the schematic diagrams is to effect a conceptual separation of biological (population) subunits coupled by behavioral interactions.

**APPENDIX II**

**POPULATION BALANCE EQUATIONS AS A POSITIVE FEEDBACK SYSTEM**

The linearized population balance equations can be cast in a conventional feedback form. Consider the autonomous system

\[
\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)n,
\]

\[
n(0, a) = n_0(a),
\]

\[
n(t, 0) = \int_{a'}^a b(a')n(t, a')\, da'.
\]

Taking time Laplace transforms and solving the above system one obtains

\[
\hat{n}(s, a) = \frac{\sigma(a)e^{-as} \int_0^a e^{s\xi}[n_0(\xi)/\sigma(\xi)]\, d\xi}{1 - \int_0^a e^{-s\xi}\phi(\xi)\, d\xi},
\]

where \(\sigma(a) = \exp[-\int_0^a \mu(a')\, da']\) is the probability of surviving to age \(a\), and \(\phi(a) = \sigma(a)b(a)\) is the net reproductive rate (Langhaar 1972, Keyfitz 1968). If we integrate both sides over all ages, then

\[
\hat{N}(s) = \frac{\hat{n}(s)}{\hat{\phi}(s)},
\]

where \(\hat{\phi}(s) = \int_0^a e^{-s\xi}[n_0(\xi)/\sigma(\xi)]\, d\xi\) and \(\hat{\phi}(s)\) is the transform of the net reproduction rate. We can write this as

\[
\hat{N}(s)/\hat{\phi}(s) = \hat{n}(s)/(1 - \hat{\phi}(s)),
\]

which corresponds to the positive feedback system shown in Fig. 11.

Thus, as pointed out previously, each population behaves as a positive feedback system. The question of ecosystem stability is particularly intriguing from this standpoint, since the community is then viewed as an interconnection of inherently unstable subunits. In this light, it is perhaps not so surprising that population abundance appears rather loosely regulated in nature, since the interconnections are quite flexible behavioral algorithms, or that new immigrants can be especially disruptive to a coevolved ecosystem.

**APPENDIX III**

**SOLUTION TO THE DENSITY EQUATIONS**

The population-balance equations are first-order hyperbolic, and so may be treated by the method of characteristics (Sneddon 1957, Courant and Hilbert 1962, Friedly 1972). For convenience we record their solution here; a more complete discussion may be found in Langhaar (1972) or Trucco (1965a, b).

The partial differential equation for \(n(t, a)\)

\[
\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(t, a)n
\]

(III.1)

is equivalent to the set of ordinary differential equations

\[
dt/1 = da/1 = dn/-\mu n.
\]

(III.2)

The solutions to this set are the characteristic trajectories. Projected on the \((t, a)\) plane, called a Lexis Diagram (Keyfitz 1968), they trace out the life history of
a cohort, a group of individuals born simultaneously. Their solution for the linear case noted is just

\[ n(t, a) = \text{constant} \times \exp \left\{ - \int_{t}^{a} \mu(t, a') \, da' \right\}, \]  

(III.3a)

\[ a = t + \text{constant}. \]  

(III.3b)

The complete solution surface \( n(t, a) \) is swept out by the characteristic curves if initial conditions are provided which are transverse to the characteristics. The initial conditions for equation (III.1) are supplied in two parts:

(a) the age distribution of the "original settlers," \( n(0, a) \);

(b) the "native born" birthrate \( n(t, t) = \int b(t, t') n(t, a') \, da' \).

The initial distribution affects only the portion of the solution lying in the upper diagonal of Fig. 12A where \( a > t \), whereas the birthrate boundary condition is effective only when \( a < t \). Therefore, we must write the solution to equation (III.3b) in two parts (Fig. 12A).

\[
\begin{align*}
    a & = \begin{cases} 
    t + a_1 & (a > t) \\
    t - t_0 & (a < t)
    \end{cases} \\
    a_1 & = \text{initial age at } t = 0 \text{ of an individual in the original population} \\
    t_0 & = \text{time of birth of a new individual into the population.}
\end{align*}
\]

(III.4)

The complete solution to (III.1), using (III.3a) and (III.4) is

\[
n(t, a) = \begin{cases} 
    n(0, t-a) \exp \left\{ - \int_{t}^{a} \mu(\eta, \eta + a - t) \, d\eta \right\} & (a > t) \\
    \frac{\Delta}{n(0, t-a)} \sigma(t, t-a) & (a < t)
    \end{cases}
\]

where \( \Delta \) is the domain of integration as shown in Fig. 12B. The solution surface for a periodic birthrate may be visualized as shown in Fig. 13, where \( t = \text{constant slices} \) show the instantaneous shape of the age profile, and diagonal sections, \( a = t \), show the shape of the survivorship of a cohort.

APPENDIX IV

SOLUTION TO A HOST-PARASITE-SYSTEM MODEL:
POINT BIRTH, PARASITISM IN EGG STAGE

Linearization of equations (14) and (15):

Let \( h_e \) and \( \Delta h \) be equilibrium values of \( h_e(t) \) and \( \Delta h(t) \), respectively, and introduce small deviations, \( X_e(t) \) and \( X_h(t) \), such that

\[ h_e(t) = h_e + x_h(t), \quad \Delta h(t) = \Delta h + x_h(t). \]  

(IV.1)

We also introduce an input, \( u(t) \), in the birthrate of the host

\[ b_h(t) = b_h + u(t), \]  

(IV.2)

where \( b_h \) is a fixed, nominal value. Since \( \Delta h(t) \) is the egg fraction of the parasite population, the adult population at age \( \alpha_p \) is given by

\[ p(\alpha_p, t) = p(\alpha_p) + \sigma_p x_p(t - \alpha_p), \]  

(IV.3)

where \( p(\alpha_p) \) is the equilibrium value of the population, and \( \sigma_p \) is the survivorship from age zero to \( \alpha_p \).

Substituting equations (IV.1) and (IV.2) into (15), we get

\[ h_e + x_h(t) = \left( b_h + u \right) \cdot \sigma_h \{ h_e + x_h(t - \alpha_h) - \Delta h - x_p(t - \alpha_p) \}, \]  

(IV.4)

\[ \frac{\delta h}{\delta h_e} = \frac{\delta f}{\delta h_e} \frac{\delta h}{\delta h_e} + \frac{\delta f}{\delta p} \frac{\delta h}{\delta p}, \]  

where

\[ \delta h(t) = x_p(t), \quad \delta h_e(t) = x_h(t), \quad \delta p(\alpha_p, t) = \sigma_p x_p(t - \alpha_p) \]

and the partial derivatives are evaluated at the equilibrium state. We thus have

\[ x_p(t) = c_2 x_p(t - \alpha_p) + c_3 x_h(t), \]  

where

\[ c_2 = Ah_{\rho} \sigma_p p(\alpha_p) \exp \left\{ -Ap(\alpha_p) \right\}, \]  

(IV.7)

Equation (14) at the equilibrium state is

\[ \Delta h = h_e \{ 1 - \exp \left\{ -A \sigma_p P \Delta h \right\} \}, \]  

(IV.8)

where \( \Delta h \) is related to \( h_e \) by equation (IV.5), that is,

\[ \Delta h = \{ 1 - (1/b_h a_h) \} h_e, \]  

(IV.9)

so that \( h_e \) and \( \Delta h \) can be obtained by solving these two equations which, in turn, may be substituted into (IV.6) and (IV.7) to obtain analytical expressions for \( C_e \) through \( C_i \). We find that

\[ c_0 = \frac{1}{\phi - 1} \Delta h, \quad c_1 = \phi, \quad c_2 = \kappa \log \frac{\phi}{\phi - 1}, \]  

(IV.10)
and
\[ c_3 = 1 - 1/\phi, \]  

(IV.11)

where \( \phi = b_k \sigma_3 > 1 \). Note that \( C_1C_3 = C_1 - 1 \).

The root investigation simplifies if \( a_3 = a_9 \). Letting
\[ e^{ia_3} = e^{i\alpha} = z \]
and noting that \( C_3 > 1 \) and \( C_1C_2 = C_1 - 1 \), equation (18) reduces to a quadratic equation for \( z \):
\[ z^2 - (1 + c_2)z + c_1c_2 = 0. \]

The characteristic equation in the \( z \)-domain may be rewritten in the following factored form:
\[ 1 - c_2 \frac{z - c_1}{z(z - 1)} = 0. \]

(IV.12)

The root-locus when \( C_2 \) is changed from zero to infinity, while keeping \( C_3 \) at a constant value (which must be greater than one for the ecosystem to be meaningful) is sketched in Fig. 14. It can be seen that there exists a certain range in \( C_2 \) where the roots will be conjugate complex. Suppose that in this range
\[ z_1, z_2 = \sigma \pm i\omega, \]
then
\[ e^{ia}\sigma = \sigma \pm i\omega, \]
so that its root, \( s \), will have an imaginary part which, in turn, means a resonance peak appears in its frequency response.

The adult parasite population is computed by integrating equation (26) and solving for \( P \). The solution is written in (27) as
\[ P(s) = G_1(s)H_0(s), \]
where
\[ G_1(s) = \frac{c_2}{c_2} \left[ e^{-(\mu_2+\gamma_2)}(a_9 + 1) \gamma_0 \right] \left[ e^{-(\mu_3+\gamma_3)}(a_9 + 1) \gamma_0 \right], \]
so that \( X_\phi(s, a) \) can be written as
\[ X_\phi(s, a) = (c_1G_1(s) + c_2)e^{-(\mu_3+\gamma_3)}H_0, \]
and the total parasite population, \( Y_\phi(s) \), is given in equation (28).

Equations (29) and (30) for the host population can be solved by integrating successively over the age segments: \( (0, \alpha_3), (\alpha_3, \alpha_3 + \gamma_3), \alpha_3 + \gamma_3, \alpha_3 \); we obtain
\[ H_0(s) = e^{-(\mu_3+\gamma_3)}(a_9 + 1) \left[ \frac{1 + e^{-(\mu_3+\gamma_3)}}{\mu_3 + s} \right] \left[ c_2H + kU \right] + \frac{rP}{\mu_3 + s} \left[ \frac{1 + e^{-(\mu_3+\gamma_3)}}{\mu_3 + s} \right], \]

\[ \Delta = G_8(s)H(s) + G_4(s)P(s) + G_5(s)U(s), \]

(32)

\[ H(s) = kU(s) \left[ \Gamma \frac{rP}{1 - \Gamma} \right] \left[ e^{-(\mu_3+\gamma_3)}(a_9 + 1) \gamma_0 \right] \left[ e^{-(\mu_3+\gamma_3)}(a_9 + 1) \gamma_0 - 1 \right], \]

\[ \Delta = G_6(s)P(s) + G_7(s)U(s), \]

where
\[ \Gamma = \frac{1 - e^{-(\mu_3+\gamma_3)}(a_9 + 1) \gamma_0}{\mu_3 + s} \]
and:
\[ Y_\phi(s) = \frac{c_2}{\mu_3 + s} \left[ \frac{1 + e^{-(\mu_3+\gamma_3)}}{\mu_3 + s} \right] \left[ \frac{1 + e^{-(\mu_3+\gamma_3)}}{\mu_3 + s} \right] P, \]

\[ \Delta = G_6(s)H(s) + G_7(s)P(s) + G_10(s)U(s). \]

The resulting set of linear equations (27), (28), (32), and (34) can be solved to obtain
\[ H_0(s) = \frac{G_5G_1 + G_6}{1 - G_1(G_5G_6 + G_4)} U(s), \]

\[ P(s) = \frac{G_1G_3G_5 + G_2G_5}{1 - G_1(G_5G_6 + G_4)} U(s), \]

\[ H(s) = \frac{G_1G_3G_5G_7 + G_1G_3G_6 + G_7}{1 - G_1(G_5G_6 + G_4)} U(s), \]

\[ \Delta = K_\phi(s)U(s). \]

The characteristic equation for \( Y_\phi(s) \) is therefore
where \( G_i(t), i = 1, 3, 4, 6 \) are defined above.

Even for this relatively simple linear model, the resulting characteristic equation is much too complex to be employed in equations (36). Our interpretation of, of course, is not unique, since the analysis proceeds by linearization, only the values of the linearization constants change in altering the model.

For a herbivore, \( h(t,a) \), feeding on a resource, \( R(t) \), it is sensible to measure \( R(t) \) in units of leaf area or biomass, so as to reflect the nature of the consumption of \( R(t) \) by \( h(t,a) \). In general, (36a) will have the form:

\[
\frac{1}{R(t)} \frac{dR(t)}{dt} = \text{Birth} - \text{Death} = B(R, H, u) - D(R, H, u), \quad (VI.1)
\]

where \( H(t) = \int_0^t h(t,a) \, da \) is the herbivore population and \( u(t) \) is the periodic environmental forcing. Suppose that, in the absence of herbivore consumption, the resource death rate exhibits simple linear density control: \( D = \mu_0 + \mu H \cdot 1/(\eta + R) \) (VI.2), where \( \eta, \mu > 0 \) are constants.

The resource birthrate is presumed periodic (seasonal) and density dependent, so takes the form

\[
B = b_0 + \beta u(t) - b_1 R. \quad (VI.3)
\]

However, the periodic influence \( u(t) \) should affect birth and death rates in opposite directions, so (VI.2) should be modified to

\[
D = \mu/(d + u(t)) + \mu H \cdot 1/(\eta + R). \quad (VI.4)
\]

The modified logistic equation for resource growth is therefore

\[
\frac{1}{R} \frac{dR}{dt} = \left[ (b_0 + \beta u(t) - b_1 R) \right. \left. - \left( \frac{\mu}{d + u(t)} + \mu H \cdot 1 \right) \right]. \quad (VI.5)
\]

The equilibrium resource level in the absence of herbivore consumption and periodic forcing is

\[
R(u = 0, H = 0) = \frac{-\mu}{b_1}. \quad (VI.6)
\]

Equation (VI.5) can be normalized and linearized in the usual fashion to yield equation (37).

For simplicity, we suppose that the herbivore has an alternate food supply which, in the absence of resource \( R(t) \) will sustain him. Therefore, we can assume that the abundance of \( R(t) \) will enhance the birthrate of \( h(t,a) \) up to some limit, but not significantly affect the death rate. Therefore, we write

\[
h(t,0) = b R/(\eta + R) \int_0^t h(t, a) \, da, \quad (VI.7)
\]

where \( b \) is a constant which scales the birthrate enhancement according to consumption. If (VI.7) is linearized about the equilibrium population and resource levels, one obtains equation (40).

For the case of finite birth window, \( \gamma \), the characteristic equation, (49), can be written:

\[
\rho e^\hat{\epsilon} = h_0(1 - e^{-\hat{\epsilon}}),
\]

where

\[
\rho = (s + \mu) \alpha, \quad \hat{\epsilon} = \gamma/\alpha.
\]

The roots at \( -\hat{\epsilon} \) and \( -\mu \) remain unchanged, but the investigation of the remaining root locus requires considerable effort. A detailed analysis, however, reveals a critical dependence on the breeding window width, \( \gamma \), as mentioned in the text, leading to a bifurcation near \( \gamma = \alpha \).

LITERATURE CITED


