APPLICATIONS OF DISCRETE AND CONTINUOUS NETWORK THEORY TO LINEAR POPULATION MODELS[1]

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Abstract. The well-established methods of network construction and analysis are adapted to the problem of modeling single populations. A major advantage of the resulting approach is that it allows explicit incorporation of key processes in the life cycle of the organism being modeled, with feedback loops providing economy of representation where they are allowed. Thus, network structures provide heuristic vehicles by which population models can be developed and modified. When a model is linear and has parameters that do not vary with time, a characteristic dynamic function can be derived by inspection from a simple transform of the network representation. The zeros of the function can be found (analytically or by commonly available numerical methods) and used directly to deduce the modeled population's dominant growth pattern and its propensity to sustain oscillations. In addition, under certain conditions (i.e., that the network model not contain both time delays and integrators), a straightforward method (partial fraction expansion) is available for deduction of the modeled population's specific responses to a variety of perturbations.

Key words: Life cycle models; network analysis; network models; population dynamics; population models; population waves; time delays.

INTRODUCTION

From a population dynamics point of view, the two processes associated with the individual organism that are most important are survival and reproduction; and state variables of the individual (e.g., physiological, anatomical and behavioral variables) often are considered important only to the extent that they affect those two processes. Since many of the variables that affect survival usually are very strongly correlated with age, many population models (e.g., the standard matrix model [Lewis 1942, Leslie 1945], the renewal equation [Feller 1941], and the von Foerster [1959] model) are based on state spaces in which the states of the individual members are described entirely in terms of their ages. Because age simply is a measure of time, initialized at or close to the birth of the individual, and since the progression of time conventionally is taken to be deterministic, the description of states in terms of ages is especially convenient. However, if the state space based on age is the only one available to a modeler, then his hypothetical constructions and idealizations will be rather severely constrained. This paper is an attempt to broaden the modeler's horizons slightly by showing that time initialized by events other than birth can be used as the basis of a rather more adaptable state space. In this space, one may have explicit representations not only of time since birth, but also of such variables as time since the last ovulation, time since impregnation, and time

since parturition. Thus, observable parameters such as time to maturity, ovulation interval, and durations of postmating and postpartum regression or of nonreproductive lactation can be incorporated explicitly in the models and their consequences with respect to population dynamics deduced. The models themselves can be formulated and modified through the extremely heuristic techniques of network construction.

Once the model is formulated in network form, the next step is to deduce the dynamic behavior implicit in it. This can be done on an ad hoc basis (e.g., for specific perturbations) through analog or digital simulation (not described herein) or a more general basis through a combination of the very powerful but simple methods of linear transforms and linear flow graph analysis, which are described in this paper. This combination of methods applies to linear systems whose parameters are lumped and constant (independent of time) and that are deterministic insofar as only the expected values of the population are carried (see Oster and Takahashi [1974] for applications of linear transforms to population models with distributed parameters). These same limitations also apply to the vast majority of the body of systems theory as it exists today. The usual rationale for the extensive development of that body to begin with and for its continued refinement and expansion, in spite of these limitations, is the fact that many real systems conform reasonably well to the limitations and many additional systems conform in the short-term or for small perturbations about specified points and thus have dynamic be-

haviors that can be deduced reasonably well by judicious piecewise or limited application of the theory. What can we attempt to deduce about a real population from a theory limited to lumped-parameter, time-invariant-parameter, linear systems? It certainly is well known that, among other things, we can use such a theory to deduce the tendency (under given hypothetical parameter values, perhaps innately determined, perhaps determined by ecological context) of a population to shift away from or toward a presumed stable value (Rosenzweig and MacArthur 1963). Similarly, we can use it to deduce the tendency of a population, under given circumstances, to sustain waves (Keyfitz 1972); and, we can use it to deduce the frequency of those waves (Oster and Takahashi 1974). We also can use it to deduce the responses of the modeled population to a wide variety of small perturbations. Finally, we can use it to deduce the sensitivities of these tendencies and responses to the various life-history parameters represented in the model.

NETWORK MODELS BASED ON CONTINUOUS TIME

When models are constructed on state spaces based on initialized time, it often is convenient to lump certain sets of contiguous states together into time delays of various lengths. When this is done, the concept of flow is especially useful for bookkeeping of the conservation relationships (Lewis 1972). An individual might be considered to have entered such a set at the time of birth, on reaching a certain age, on becoming pregnant, at the time of ovulation, on giving birth, or at any other specified event. Correspondingly, an individual would be considered to have left the set on reaching a certain age (e.g., the age of sexual maturity), on termination of pregnancy, at the time of subsequent ovulation, on completion of lactation or regression, or at any other appropriate time. When such lumped states are used, the modeler is concerned with the rate at which individuals are entering a given process (such as maturation, gestation, lactation, regression, and the like), idealized to be of fixed duration, and the rate at which they are emerging from it on completion; but he is not concerned with the total number of individuals involved in the various stages of the process. Therefore, he is interested in the flow of individuals into the process and the flow of individuals out of the process. If entry into the process and emergence from it are signaled by discrete events, the input and output flows are discrete functions of time, comprising series of delta functions. For the idealized process of fixed duration, the salient conservation relationship is

$$J_{out}(t) = K J_{in}(t - T) \qquad (1)$$

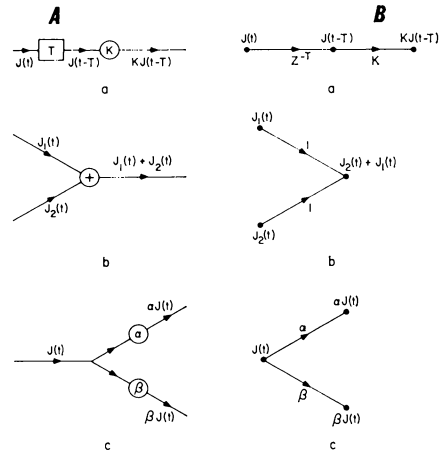where $J_{in}(t)$ is the flow into the process at time t,

FIG. 1A. Network symbols for (a) a pure time delay, T, with a scalar, K; (b) an adder; and (c) a branch point, which is conservative if $\alpha + \beta = 1$, nonconservative otherwise.

FIG. 1B. Linear flow graph symbols for the corresponding network elements of Fig. 1A.

$J_{out}(t)$ is the flow out of the process at time t, T is the duration of the process, and K is the proportion of those entering the process at $t\text{-}T$ that survive to emerge at t. Note that the distribution of expected mortality over the interval T is not necessarily specified; therefore, one does not necessarily know the actual number of individuals represented as being involved in the total process or any of its various stages.

The conventional network representation of such a set of lumped states is shown in Fig. 1Aa and consists simply of a pure time delay element (labeled T in the figure) drawn in series with a scalar element (labeled K) (Cadzow 1973). Continuing with this pattern, where flows are indicated by directed paths and operations on those flows (such as delaying or scaling) are indicated by elements connected by those paths, one needs an adder for the conservative convergence of two or more paths (Fig. 1Ab) and a simple branch point for the conservative or nonconservative divergence of paths (Fig. 1Ac). With these five structures, one can construct a very large number of interesting population models (Lewis 1972). For the purposes of this paper, however, the discussion will be limited to models in which the proportionality factors in all of the scalars are constant, in which case the models are linear, with time-invariant parameters.

The development and analysis of models employing these and other, subsequently introduced structures will be illustrated through a series of idealized examples embodying many of the life-history parameters commonly observed and recorded for vari-

ous animal species (e.g., Lack 1954, Clark et al. 1967, Bent 1968, Sadleir 1973).

Example 1

A population consists of identical protozoans that reproduce solely by binary fission and require no conjugation. The culture medium is sufficiently well regulated that the time between successive fissions is constant, T_F. Death is a nonselective, Poisson process, with the probability of survival of an individual over any interval T being given by e^{-mT}.

A network embodying the dynamics of this population is shown in Fig. 2Aa, where J_0 is the flow of newly formed fission products into the population and J_1 is the flow of surviving adults into fission.

Example 2

The female members of a population of idealized mammals exhibit the following life cycle. Each newborn female requires 300 days to reach sexual maturity, signaled by her first ovulation. Subsequently, she ovulates once every 20 days and at each ovulation she faces the same, fixed probability, K_1, of becoming pregnant. Gestation requires 38 days and the expected number of female offspring per successfully completed pregnancy is 3.7. Fifteen days after parturition, the first postpartum ovulation occurs, signaling the return of the 20-day ovulation cycle. The expected proportion of newborn females surviving to sexual maturity is K_2; having reached maturity, the females face a nonselective death process, with probability e^{-mT} than any given individual survives an interval of duration T.

A network model embodying the dynamics of this population is shown in Fig. 2Ab, which depicts six components of flow. J_0 is the flow of newborn female offspring into the population. J_2, the total flow of ovulating females, comprises the flow, J_1, of those ovulating for the very first time, the flow, J_6, of those ovulating for the first time since parturition, and the flow, J_3, of those that failed to become pregnant during their last ovulation and simply have passed through the normal ovulation cycle. J_4 is the flow of newly impregnated females into gestation; J_5 is the flow of females emerging from gestation. The flow of newborn females is 3.7 times the flow of females completing gestation.

Example 3

The female members of a population of idealized sea birds exhibit the following life cycle. Nesting occurs in the fourth month of every year. A newly-fledged female faces probability K_1 of surviving to age 36 mo, at which time she is sexually mature and capable of participating in nesting for the first time.
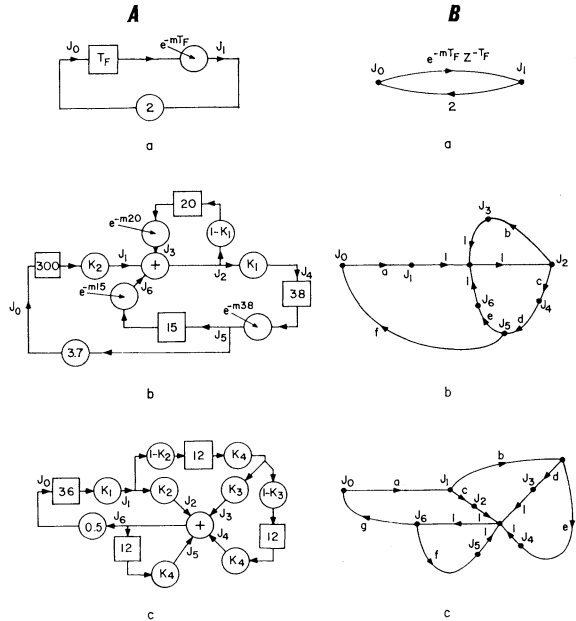

FIG. 2A. Network models of idealized animal populations.
(a) Binary fission with fixed interfission interval.
(b) Periodic ovulation in an idealized mammal population.
(c) Annual nesting in an idealized seabird population.
FIG. 2B. Linear flow graphs corresponding to the networks of Fig. 2A.
(b) $a = K_2 z^{-300}$; $b = e^{-m20}(1 - K_1)z^{-20}$; $c = K_1$;
$\quad d = e^{-m38}z^{-38}$; $e = e^{-m15}z^{-15}$; $f = 3.7$.
(c) $a = K_1 z^{-36}$; $b = K_4(1 - K_2)z^{-12}$; $c = K_2$; $d = K_3$;
$\quad e = K_4(1 - K_3)z^{-12}$; $f = K_4 z^{-12}$; $g = 0.5$.

The probability that she will do so is K_2. Once she has participated in nesting, she will continue to do so every spring for the rest of her life. If she did not nest during her first adult season, the probability is K_3 that she will do so in her second; failing this, she is virtually certain to nest in her third. All adult birds face probability K_4 of surviving from the end of one nesting season to the end of the next. Each nesting female produces one fledged brood per season, with 0.5 female fledglings expected per brood.

A network model embodying these dynamics is shown in Fig. 2Ac. Here J_0 represents the flow of female fledglings into the population; J_1 represents the flow of newly emerging adult females; J_6 is the flow of females through nesting and comprises J_2 (the flow of 3-yr-old nesters), J_3 (the flow of first-time, 4-yr-old nesters), J_4 (the flow of first-time, 5-yr-old nesters), and J_6 (the flow of returning birds that nested the previous year). The flow of fledged offspring is 0.9 times the flow of females through nesting.

As one can see from the previous examples, the five network structures introduced so far allow con-
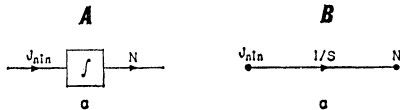
FIG. 3A. Network symbol for an integrator.
FIG. 3B. Linear flow graph symbol for an integrator.

struction of fairly complex and interesting models. The addition of a sixth structure, namely the integrating element shown in Fig. 3A, makes the linear modeling capabilities even broader. When individuals in different age or other initialized time classes are considered to be equally subject to the same stochastic processes, such as becoming pregnant, being preyed upon, becoming infected, and the like, then it often is convenient to combine them into a single pool in the model. For models based on continuous time, the integrator provides the vehicle for such pooling. The conservation relationship represented is

$$N(t) = \int_{-\infty}^{t} J_{nin}(t) \ dt \qquad (2)$$

where $N(t)$ is the number of members of the pool at time t, and $J_{nin}(t)$ is the net flow of individuals into the pool at t.

Example 4

The females of a population of idealized insects exhibit the following life cycle. The newly-hatched female requires 90 days to progress through the various immature stages and reach sexual maturity, at which time she joins a breeding pool and produces an average of K_2 female eggs per day. Hatching takes 30 days, and the proportion of female eggs expected to survive to adulthood is K_1. Adults face a nonselective death process, with probability K_3 of surviving each day.

A network model embodying these features is shown in Fig. 4Aa. Here J_0 is the flow of newly produced female eggs; J_3 is the net flow of members into the breeding pool and comprises the difference between the flow (J_1) of newly emerging adult females and the flow (J_2) of females out of the pool as a result of death; N is the total membership of the pool. The death rate, δ, and egg-production rate, β, are given by the following equations:

$$\delta = |\log K_3|/T_{\text{day}} \qquad (3)$$

$$\beta = |\log K_2|/T_{\text{day}} \qquad (4)$$

where T_{day} is the number of time units in 1 day.

So far, the examples have been restricted to situations in which the lumped states (initialized time classes) were based on single processes. In other words, according to the idealized life cycle specifications, an individual member of a population could
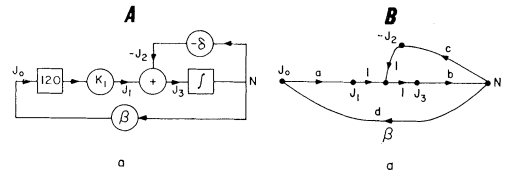

FIG 4A. Network models of idealized animal populations.
  (a) Breeding pool in an idealized insect population.
  (b) Same insect population, but with age-dependent mortality: $\gamma' = (K_3')^{180}$; $\gamma'' = (K_3'')^{180}$.
FIG. 4B. Linear flow graphs corresponding to the networks of Fig. 4.
  (a) $a = K_1 e^{-120s}$; $b = 1/s$; $c = -\delta$; $d = \beta$.
  (b) $a = K_1 e^{-120s}$; $b = \gamma' e^{-180s}$; $c = 1/s$; $d = -\delta'$; $e = f = \beta$; $g = 1/s$; $h = -\delta''$; $i = -\gamma'' e^{-180s}$.

be represented as being involved in only one process at any given moment. On the other hand, there are numerous ways in which idealized or hypothetical life cycles could be specified that would require states based on two or more processes. Suppose, for example, that an individual female can be lactating and gestating at the same time. One very well might wish to include in his model the possibility that survival from day to day is different for lactating individuals (being forced to defend the litter), pregnant individuals (being hampered by physiological state) and individuals that are both pregnant
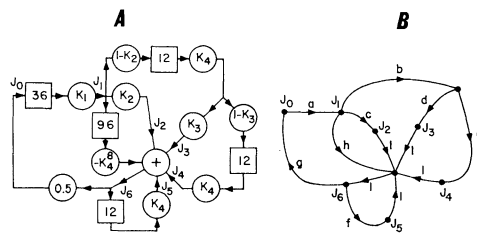

FIG. 5A. The model of Fig. 2c, with absolute longevity of 11 yr.
FIG. 5. Linear flow graph corresponding to network of Fig. 5:
  $a = K_1 z^{-36}$; $b = K_4(1 - K_2)z^{-12}$; $c = K_2$; $d = K_3$; $e = K_4(1 - K_3)z^{-12}$; $f = K_4 z^{-12}$; $g = 0.5$; $h = -K_4^8 z^{-96}$.

and lactating (having both handicaps simultaneously). Furthermore, one might wish to include also the possibility that the probability of impregnation is different for lactating and nonlactating females, or that it varies from stage to stage during lactation. Even more commonly, one might wish to include age as well as other initialized-time variables in the state description, on the assumption that mortality or natality was affected significantly by age as well as participation in the other processes. Under certain, rather restricted circumstances, such specifications can be represented explicitly and economically with network models of the type discussed in this paper. In general, however, these network models are not well suited for such complex specifications.

Example 5

The females of Example 4 exhibit age-dependent mortality such that during the first 180 days after reaching maturity, the individual faces an effectively constant probability, K_3', of surviving each day, for the second 180 days she faces a different probability, K_3'', and her maximum longevity is 360 days from maturation.

Figure 4Ab shows a modified version of the network in 4Aa, embodying these new features. Here, J_3' is the net flow of members into the younger breeding pool and comprises the difference between the flow (J_1') of newly emerging adult females and the flows (J_2' and J_4') of females out of the pool as a result of death and of graduation to the older breeding pool, respectively. J_3'' is the net flow into the older breeding pool and comprises the difference between the flow (J_1'') of newly graduating individuals and the flows (J_2'' and J_4'') of individuals out of the pool as a result of death.

Example 6

The females of Example 3 face essentially nonselective mortality (as stated in the example), but only until age 11, their absolute longevity, beyond which there are zero survivors.

Figure 5A shows the appropriate modification of the network in Fig. 2Ac. As in Example 5, double bookkeeping accomplishes the task. The flow of emerging 3-yr-old females passes into a 96-mo delay; the proportion, $K_4{}^8$ that survive the corresponding 8 yr (to the limit of longevity) is subtracted from the flow of nesting adults.

Example 7

The same idealized seabirds exhibit completely age-dependent mortality and natality, with proportion p_i surviving from the end of the $i-1$ nesting season to the end of the ith nesting season, and f_i female fledglings expected per brood of females participating
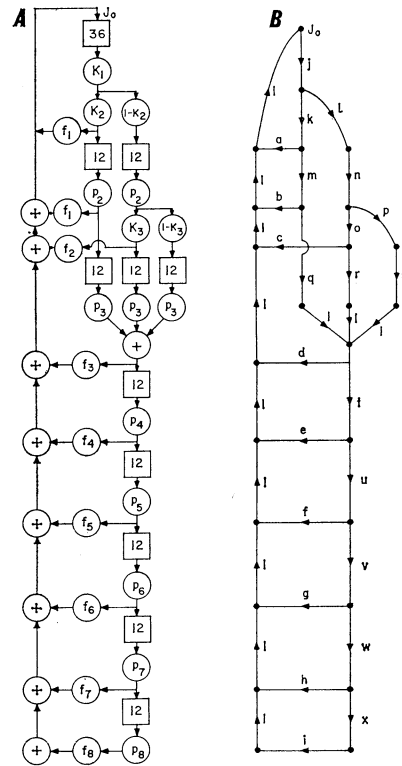

FIG. 6A. The same model, with age-dependent mortality throughout.

FIG. 6B. Linear flow graph corresponding to the network of Fig. 6:

$a = f_1; \; b = f_2; \; \ldots i = f_8; \; j = K_1 z^{-30}; \; k = K_2; \; l = 1 - K_2;$
$m = n = p_2 z^{-12}; \; o = K_3; \; p = 1 - K_3; \; q = r = s = p_3 z^{-12};$
$t = p_4 z^{-12}; \; u = p_5 z^{-12}; \; \ldots x = p_8 z^{-12}.$

in their ith nesting season. Once again, the absolute longevity is 11 yr.

A network realization of this idealized life cycle is shown in Fig. 6A. For their first two nesting seasons, the birds are represented in diverging paths, one for third-year primiparae, one for fourth-year primiparae, and one for fifth-year primiparae. The three parallel paths in Fig. 6A can be combined to yield the simpler version of Fig. 7A. Except for its first time delay, this network simply is a form of the Leslie model (Lewis 1942, Leslie 1945). The scale factors $K_2 f_1$, $(K_2 + K_3 - K_2 K_3)$ $f_2, f_3, f_4, \ldots, f_i$ would be the elements of the first row of the Leslie matrix, and the scale factors $K_1, p_2, p_3, p_4, \ldots, p_i$ would be subdiagonal elements.

Example 8

Mortality among the females in the idealized population of Example 2 depends on the age of the individual and upon whether or not she is pregnant. The absolute longevity is $\approx 2,000$ days.

Suddenly, with a very simple change in the statement of the life cycle, the problem is transformed
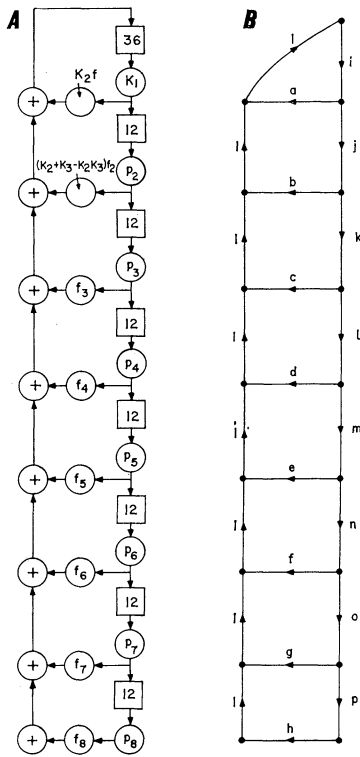
FIG. 7*A*. A Leslie-model equivalent of the network of Fig. 6.

FIG. 7*B*. Linear flow graph corresponding to the network of Fig. 7:

$a = K_2 f_1$; $b = (K_2 + K_3 - K_2 K_3) f_2$; $c = f_3$; $d = f_4$; ... $h = f_8$; $i = K_1 z^{-36}$; $j = p_2 z^{-12}$; $k = p_3 z^{-12}$ ... $p = p_8 z^{-12}$.

from one quite tractable in terms of networks to one for which the value of the network approach is extremely doubtful. The reason for this simply is that there are too many states of the individual that must be distinguished. Except for those representing flow of newborn offspring, no feedback loops will be allowed in the network, since they obscure age. Furthermore, at the time of each ovulation, each female faces a branching point with respect to state. If she becomes pregnant and survives, her next ovulation will occur 53 days later. If she does not become pregnant, but survives, she will ovulate again in 20 days. This branching converts ovulation from an idealized process with a period of 20 days to a process with a fundamental period of 1 day (the greatest common divisor of 20 and 53). In a truly continuous time base, the probability that any two values of time actually have a greatest common divisor is essentially zero. Therefore, one normally would expect branching to convert periodic processes into totally aperiodic processes. In the case at hand, the temporal resolution of the life cycle statement was tacitly set at 1 day, imposing a minimum period of 1 day on all processes involved and thus masking

the inherent aperiodicity. Effectively, then, the periodic process of ovulation is made aperiodic by the branchings. This aperiodicity of the timing of state changes precludes feedforward paths in the network (i.e., convergence of paths in the network).

Without feedback or feedforward paths, the portion of the network representing the state of the adult female will comprise an ever expanding tree, with a branching point representing each ovulation and one branch emanating from that point for each of the two possible states following ovulation. The complete network is utterly impractical to draw. Since, fortuitously, the network has a basic periodicity of 1 day, it can, in principle but with considerable difficulty, be reduced to the Leslie-Lewis form and represented by a Leslie matrix. On the other hand, if ovulation had been specified as being aperiodic with no implied unit of temporal resolution (e.g., induced ovulation), then reduction to the Leslie-Lewis form would not be a precise realization of that model. Furthermore, the expanded tree in this case would have an infinite number of branch points spaced infinitesimally close together. In such cases, conventional network techniques offer no conceptual advantages over other mathematical and simulation methods.

NETWORK MODELS BASED ON DISCRETE TIME

It is not at all difficult to argue for the validity of discrete-time models. In the first place, even with the most modern clocks, there always is a practical limit to the resolution of time. Furthermore, because the states of individual organisms cannot be measured instantaneously, but require certain spans of time for their determination, there is a tradeoff between precision in time and precision of state determination. At the heart of this tradeoff very likely lies a fundamental biological uncertainty principle, very much akin to that of modern physics. When the states of individuals over an entire population are to be observed, this tradeoff between temporal precision and biological precision undoubtedly will lead to compromise units of temporal resolution that are rather large. Since the empirical units of temporal resolution thus are finite and, in fact, rather large for biological populations, one can argue very logically that it is absurd to make the limit of temporal resolution infinitesimal in the models of those populations (i.e., to base them on continuous time).

From the point of view of analysis and simulation, models with fixed delays that are based on discrete time have certain advantages over the same models based on continuous time. In the first place, when time delays and pools occur together in a model, its analysis will lead to differential-difference equations if it is based on continuous time and to pure differ-

ence equations if it is based on discrete time. With presently available methods, the latter are very easy to solve completely (i.e., determine the complete response to a more or less arbitrary input), the former are quite difficult (Bellman and Cooke 1963, Hale 1971). The two types of equations usually are equally easy to analyze in terms of deduced tendencies of the system to grow or decline and to sustain oscillations. The discrete-time models have the added advantage that they can be viewed directly as flow charts for digital simulation programs.

Linear, time-invariant discrete-time network models can be constructed with five of the six structures of the continuous-time models: the pure time delay, the scalar, the adder, the directed path, and the branch point. The sixth structure of the continuous-time models, the integrator, is replaced by its discrete-time analog, the accumulator, which is illustrated in Fig. 8Aa. The appropriate conservation relationship is

$$N(\tau) = \sum_{\tau=-\infty}^{\tau} J_{nin}(\tau) \qquad (5)$$

where $N(\tau)$ is the number of members of the pool represented by the accumulator and is a function of discrete time, τ; $J_{nin}(\tau)$ is the net flow of members into the pool. Although other conventions are perfectly acceptable, it will be assumed here that the values of $N(\tau)$ and $J(\tau)$ are determined only for integral values of τ. Thus, $N(\tau)$ and $J(\tau)$ both can be considered to comprise delta functions distributed periodically with interval equal to the unit of resolution of τ. Thus, $J(\tau)$ and $N(\tau)$ are commensurate and one can restate the accumulator's conservation relationship as follows:

$$N(\tau) = N(\tau-1) + J_{nin}(\tau), \qquad (6)$$

which leads to the network equivalent shown in Fig. 8Ab, where the accumulator has been replaced by a feedback loop with a pure delay, one unit of resolution in duration.

Example 9

The females of a population of idealized mammals exhibit the following life cycle, resolved to 1 day. A newly-weaned female requires 300 days to reach sexual maturity, after which she is receptive and capable of ovulation. Ovulation does not occur spontaneously, but is induced by mating. If mating does not lead to conception, there is a 25-day period of regression, during which ovulation cannot recur and the female is not receptive. Gestation requires 35 days and is followed by a 20-day period of lactation, during which time the female is neither receptive nor capable of ovulation, and during which survival of the offspring is contingent upon survival of the mother. The probability that a receptive fe-
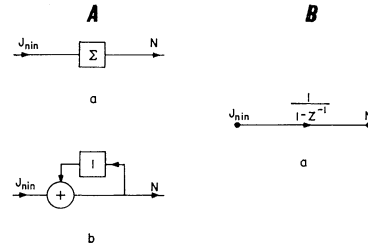

FIG. 8A. Network symbols for discrete accumulation. (*a*) An accumulator. (*b*) Equivalent network for an accumulator.
FIG. 8B. Linear flow graph symbol for an accumulator.

male mates in any given day is K_1; the corresponding conditional probability of conception is K_2. The expected number of female offspring in a newly-weaned litter is n_f. The day to day survival of the female depends upon her initialized time class, being $p_1(\tau)$ for the τth day of maturation, $p_2(\tau)$ for the τth day of regression, $p_3(\tau)$ for the τth day of gestation, $p_4(\tau)$ for the τth day of lactation, and simply p for all days during which she is receptive and capable of ovulation.

A network model embodying the dynamics of this population is shown in Fig. 9Aa. The number (N_1) of receptive females at a given day is equal to the flow (J_2) of those just completing lactation plus the flow (J_3) of those just reaching sexual maturity, plus the flow (J_4) of those just emerging from regression, plus the flow (J_5) of those that were receptive the previous day but did not mate. The daily survivorships associated with each process have been lumped into single scalars for the entire process e.g., K_6 is the product of $p_1(\tau)$ over all the days of maturation $\tau = 1$ to 300).

Example 10

The idealized life cycle of Example 4 is given with a temporal resolution of 1 day.

A network model embodying the dynamics of the population is shown in Fig. 9Ab. The number (N_A) of adult females in the breeding pool at a given day is equal to the sum of the flow (J_1) of newly emerging adults and the flow (J_2) of adults surviving from the previous day.

LINEAR TRANSFORMS FOR DYNAMIC NETWORKS

Presently, there are three major approaches to network theory: the transfer function approach, the state space approach, and the operator theory approach (Newcomb 1974, Porter 1974). The transfer function approach is probably the most thoroughly developed of these. It is based on the Fourier,
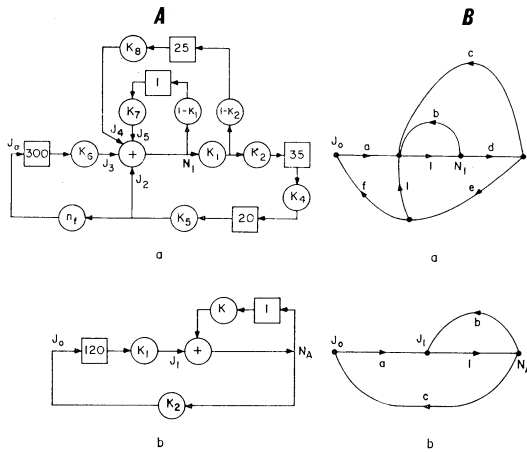
FIG. 9A. Network models based on discrete time.
(a) Idealized mammals with induced ovulation.
(b) Discrete time version of the model of Fig. 4A.,
with temporal resolution equal to one day.

FIG. 9B. Linear flow graphs corresponding to the
models of Fig. 9A.
(a) $a = K_6 z^{-300}$; $b = (1 - K_1)K_7 z^{-1}$; $c = (1 - K_2)K_8 z^{-25}$;
$d = K_1$; $e = K_2 K_4 K_5 z^{-55}$; $f = n_f$.
(b) $a = K_1 z^{-120}$; $b = K_3 z^{-1}$; $c = K_2$.

Laplace, or z transforms, depending on the circumstances; it is most directly applicable to those linear, time-invariant networks in which one wishes to relate the dynamic response of a network variable (the output or response variable) to a known or supposed segment of the time course of a network variable (the input or stimulus variable). In the case of autonomous linear networks, such as those presented so far in this paper, where there are no specified input or output connections to other networks or outside influences of any sort, the stimulus may be any known or assumed segment of the dynamics of any variable, and the response may be the resulting portion of the dynamics of any variable. Thus, the direction of causality is presupposed; stimulus causes response. In many networks, the causal roles can be reversed, but the corresponding analysis usually leads to different relationships between stimulus and response (e.g., the relationship between J_1 taken as cause and J_2 taken as effect generally will not be the same as the relationship between J_2 taken as cause and J_1 taken as effect). In many situations, it is convenient to take an initial, known segment of a given variable as cause and the resulting, subsequent dynamics of that same variable as effect; thus, the stimulus and response variables become one and the same. In all of the networks presented in this paper, every variable is causally related to every other variable; any variable could be stimulus and any other variable could be response. In such cases, certain properties of the network

transcend the specific choice of stimulus and response. These usually are generalized as the natural frequencies or eigenvalues of the network.

For linear networks based on discrete time and comprising the six structures listed in this paper, the z transform is the appropriate choice for transfer function analysis. It also is the appropriate choice for linear networks based on continuous time and comprising paths, scalars, adders, branch points, and time delays. I have found that when integrators and/or continuous stochastic time delays but no fixed time delays appear in those networks, then the Laplace transform is the appropriate choice. When both integrators and fixed time delays appear, then the Laplace transform or the modified z transform (Jury 1964) can be used, but simple analytical methods are not well developed yet.

Thorough treatments of the z and Laplace transform methods for networks are available in elementary textbooks on linear network theory and linear systems theory (Gardner and Barnes 1942, Kuo 1967, Cadzow 1973). Basically, each of these transforms converts a function of a single, real variable into a corresponding function of a complex variable (z in the case of the z transform, s in the case of the Laplace transform). For a wide variety of functions of a single variable, the transformed version is much simpler and thus represents a shorthand notation. In fact, both transforms are essentially the same as the generator functions used so commonly in probability theory. The chief advantage of the two transforms, however, lies in the fact that they convert differential equations and difference equations in the real domain into algebraic equations in the complex domain that allow the process of convolution to be carried out in the form of a simple multiplication and allow other important processes to be carried out by similarly simple algebraic manipulation. The final result in the real domain can be obtained by inverse transformation.

For those who are not familiar with these two linear transforms, their properties are summarized briefly in Table 1. A single variable, x, is used here to represent both t (the continuous time variable) and τ (the discrete time variable).

LINEAR FLOW GRAPHS

To analyze linear networks, one can transform the variables appropriately and make corresponding modifications of the operations represented by the network elements. Thus, in the cases of the network models of the 10 examples presented in this paper, the flow variables would become $J_i(z)$ or $J_i(s)$, and the pool memberships would become $N_i(z)$ or $N_i(s)$. Owing to the linearity of the transformations, the scalars, adders and branch points would be un-

TABLE 1. Some properties of the Laplace and Z transforms

Property	Function of the real variable (x)	Corresponding transform	Corresponding Laplace transform
Linearity			
Homogeneity	$kf(x)$	$kf(z)$	$kF(s)$
Additivity	$f(x) + g(x)$	$F(z) + G(z)$	$F(s) + G(s)$
Definition	$f(x)$	$F(z) = \sum_{x=0}^{\infty} f(x)z^{-x}$	$F(s) = \int_{0-}^{\infty} f(x)e^{-sx}\, dx$
Convolution			
Discrete	$\sum_{k=0}^{x} f(k)g(x-k)$	$F(z)G(z)$	NA
Continuous	$\int_{0}^{x} f(k)g(x-k)\, dk$	NA	$F(S)G(s)$
Real translation	$f(x-k)$	$z^{-k}F(z)$	$e^{-ks}F(s)$
Integration	$\int_{0}^{x} f(x)\, dx$	NA	$F(s)/s$
Summation	$\sum_{k=0}^{x} f(k)$	$F(z)/(1-z^{-1})$	NA

changed in going from the original network to its transform. The operation of the integrators in the Laplace transformed network would be represented as multiplication by $1/s$ (Table 1); the operation of the accumulators in the z transformed networks would be represented as multiplication by $1/(1 - z^{-1})$ (Table 1). A pure delay of duration T would be represented as multiplication by z^{-T} in the z transformed network or by e^{-sT} in the Laplace transformed network. Thus, pure delay, integration, and accumulation in the original networks are represented by elements akin to scalers in the transformed network, but with scale factors e^{-sT} or z^{-T}, $1/s$, and $1/(1 - z^{-1})$, respectively. A sequence of such operations in the original network would be represented by the convolution of its components, which in turn becomes the product of the corresponding scale factors in the transformed network.

For the construction of the transformed networks, it is convenient to employ linear graphs (Mason 1956, Hubbell 1973), in which the network variables (the flows and pool memberships) are represented at nodes and the operations or sequences of operations are represented as directed paths. This convention is illustrated in Figs. 1B through 9B, which show transformed versions of the networks in Figs. 1A through 9A, but in linear-flow-graph format. Note that summation is represented by convergence at a single node, branching as divergence from a single node.

There are obvious step-by-step procedures with which linear flow graphs gradually can be reduced

until there remains but one path between any variable selected as stimulus and any variable selected as response. The transformed parameter associated with that path is a concise statement of the causal relationship between the two selected variables. The more useful equivalences for linear flow graph reduction are given in Fig. 10, and in Fig. 11 they are applied to the problem of reducing the flow graph of Fig. 2Bc to a single path with J_0 as the input and J_1 as the output. Although it is reassuring to be able to carry out such manipulations, Mason (1956) published an algorithm that allows one to go directly to the final result by inspection. With his notation, the algorithm is expressed as follows:

$$P(i,j) = \frac{\{[P_1(i,j) + P_2(i,j) + \ldots + P_p(i,j)] \cdot (1-L_1)(1-L_2)\ldots(1-L_m)\}^{**}}{[(1-L_1)(1-L_2)\ldots(1-L_m)]^{*}} \quad (7)$$

where $P(i, j)$ is the parameter associated with the reduced, single path from node i to node j; $P_k(i, j)$ is the product of the parameters along the kth path from node i to node j in the unreduced flow graph (there being p such paths); and L_k is the product of the parameters around the kth closed (feedback) loop in the unreduced flow graph. Once the products are formed according to Eq. 7, all terms involving touching loops or loops and paths that touch are dropped (the asterisks serve as a reminder for this elimination of terms). Touching is defined simply as sharing any node. In Fig. 11a, for example, there is one path (a) from node J_0 to J_1 and there are four closed loops in the graph (*acg, abdg, abeg,* and *f*).
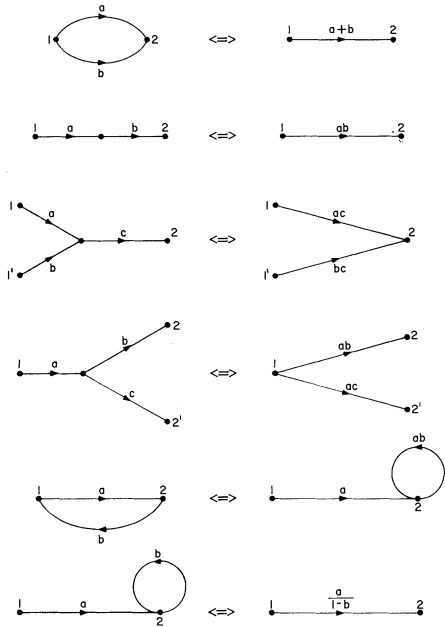
FIG. 10. Equivalences useful in systematic reduction of linear flow graphs.

FIG. 11. Step-by-step reduction of the linear flow graph of Fig. 2Ac.

The path is touched by loops *acg, abdg,* and *abeg,* but not by loop *f*. All four loops touch one another. Thus, the algorithm leads to

$$J_1(z) = \frac{a(1-f)}{1 - acg - abdg - abeg - f} J_0(z) \qquad (8)$$

which is precisely the result obtained in Fig. 11*f*. It is clear that with this simple algorithm, any of the networks presented in the examples can be reduced very quickly to a relationship of the form of Eq. 8. If one wishes to treat the stimulus and response variables as one and the same, relating the subsequent dynamics of that variable to an observed, initial segment of its behavior, then he can use the simple ploy of splitting the node associated with that variable. The only path between the resulting pair of nodes has parameter 1 associated with it; so the algorithm of Eq. 7 reduces to

$$P(i,i) = \frac{[(1-L_1)(1-L_2)\ldots(1-L_m)]^{**}}{[(1-L_1)(1-L_2)\ldots(1-L_m)]^{*}} \qquad (9)$$

where terms involving touching loops are dropped from numerator and demoninator; terms involving loops that touch node *i* are dropped from the numerator.

When Laplace or *z* transforms have been employed, $P(i, i)$ and $P(i, j)$ will be functions of *s* or *z*. The causal relationships they represent are given by

$$U_j = P(i, j) U_i \qquad (10)$$

or

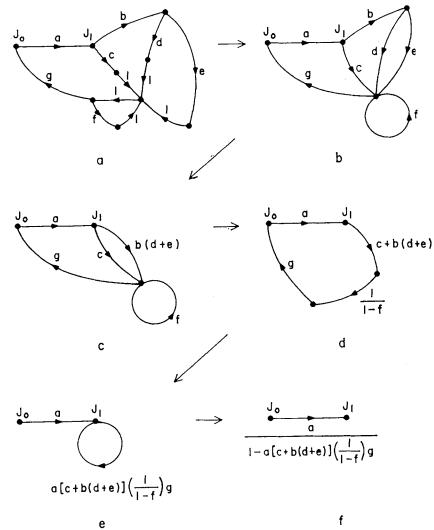$$U_i(\text{subsequent}) = P(i,i) U_i(\text{initial}) \qquad (11)$$

where U_i is the Laplace or *z* transform of the variable $[N_i(x)$ or $J_i(x)]$ associated with node *i*, and the variable on the left is taken to be effect, that on the right to be cause. As a consequence of the linearity of the networks, superposition of responses can be employed. Thus, if U_{j1} is the response of the variable at node *j* to stimulus U_{i1} at node *i*, and U_{j2} is the response to U_{i2}, then the response to U_{i1} and U_{i2} applied together is simply $U_{j1} + U_{j2}$.

Since any stimulus function can be considered to comprise a sequence of delta functions (infinitesimally close together if the stimulus function is continuous, with finite spacing if the stimulus function is discrete), the delta function itself can be considered the basic element of all stimuli. Therefore, all response functions must comprise sums of responses to delta functions; the stimulus response relationship can be characterized completely by a single delta function response. For convenience, the magnitude of the delta function eliciting the characteristic response usually is taken to be one. Such a function at any node in one of the flow graphs in this paper would represent a single individual (or unit cohort) entering or leaving a process or belonging to a pool. When the unit delta function is applied at $t = 0$ or $\tau = 0$, in these cases the response might very well be called the unit cohort response. The Laplace or transform of the unit cohort stimulus applied at $x = 0$ is equal to one. Therefore, the transform of the unit cohort response is simply $P(i, j)$ or $P(i, i)$.

To illustrate the analytical convenience of linear flow graphs with the algorithm of Eq. 7, the entries of Table 2 are the various transformed unit cohort

TABLE 2. Sample unit cohort response functions for the 10 examples of this paper

In the network of Fig.	when the variable	is a unit cohort applied at $x = 0$, the following transformed response occurs
2A a	J_0	$J_1 = \dfrac{e^{(-mT_F)} z^{(-T_F)}}{1 - 2e^{(-mT_F)} z^{(-T_F)}}$
2A c	J_0	$J_0 = \dfrac{1 - f}{1 - f - acg - abdg - abeg}$
2A b	J_1	$J_0 = \dfrac{cdf}{1 - b - ced - acdf}$
4A a	J_0	$N = \dfrac{ab}{1 - bc - abd}$
4A b	J_0	$J_0 = \dfrac{1 + b - cd - gh + cdgh - bgh}{1 + b - cd - gh + cdgh - bgh - adgf - abigf - ace + acegh + abigfcd + abgfcd}$
5A	J_0	$J_0 = \dfrac{1 - f}{1 - ahg - acg - abdg - abeg - f}$
6A	J_0	$J_0 = \dfrac{1}{1 - jka - jkmb - jkmqd - jlnoc - jlnord - jlnpsd - \ldots}$
7A	J_0	$J_0 = \dfrac{1}{1 - ia - ijb - ijkc - ijkld - ijklme \ldots}$
8A a	J_0	$J_0 = \dfrac{1 - b - dc - de}{1 - b - dc - de - adef}$
8A b	J_1	$J_0 = \dfrac{c}{1 - ac - b}$

responses for the networks of Examples 1 through 10, which were derived by inspection.

INVERSE Z AND LAPLACE TRANSFORMS

Once the z or Laplace transforms of a unit cohort response function or other network response function is available, the corresponding function of time is found by the process of inverse transformation, which can be accomplished with tables (Erdélyi et al. 1954), or, more generally, by expansion of the transformed response into additive terms of standard format (i.e., partial fraction expansion) and replacement of each of those terms by a corresponding time function of standard format. As long as integrators and fixed time delays are not both present, then by simple manipulation, it always will be possible to convert the transformed unit cohort response into a ratio of polynomials:

$$P = W/Q \tag{12}$$

$$W = a_w u^w + a_{w-1} u^{w-1} + a_{w-2} u^{w-2} + \ldots + a_0 \tag{13}$$

$$Q = u^q + b_{q-1} u^{q-1} + b_{q-2} u^{q-2} + \ldots + b_0 \tag{14}$$

where u is either s or z, w is the degree of the numerator, and q the degree of the denominator. The coefficient of u^q in Q is guaranteed to be one by the form of Eq. 7 and the fact that the z transform of the time delay is z^{-T} and the Laplace transform of the integrator is s^{-1}. The conventional partial fraction expansions comprise terms of the forms

$$c_{h,k} z^k / (z - r_h)^k \quad \text{for the } z \text{ transform} \tag{15}$$

and

$$c_{h,k} / (s - r_h)^k \quad \text{for the Laplace transform} \tag{16}$$

where r_h is the hth root of the polynomial Q, k ranges from 1 to the multiplicity of that root, and $c_{h,k}$ is a constant determined during the process of expansion. The corresponding inverse transforms are

$$c_{h,k} \binom{\tau + k - 1}{k - 1} (r_h)^\tau \quad \tau \geqslant 0 \quad \text{[for Eq. (15)]} \tag{17}$$

where

$$\binom{\tau + k - 1}{k - 1} = \frac{(\tau + k - 1)!}{(k - 1)!(\tau)!} \tag{18}$$

and τ is discrete, taking on only integral values, and

$$c_{h,k} t^{k-1} e^{(r_h t)} \quad \text{[for Eq. (16)]} \tag{18}$$

where t is continuous. Usually the multiplicity of roots is one (i.e., the roots are not repeated); so the terms of the inverse transform usually have the forms: $c_h r_h^{(\tau)}$ and $c_h e^{(r_h t)}$.

In order to apply the methods of partial fraction expansion, one first must find the roots of the polynomial Q, the denominator of the proper fraction P. This polynomial often is called the characteristic function of the network; and it is precisely analogous

to the characteristic polynomial of a matrix. In fact, the characteristic function of any network that can be reduced to the Leslie form will be one and the same as the characteristic polynomial of the corresponding Leslie matrix; the roots, r_h, are the eigen values of that matrix.

Once the roots have been found, then all that remains is to find the coefficients $(c_{h,k})$ of the expansion. When the roots are not repeated, this process is quite simple

$$r_h c_h = (z - r_h) P|_{z=r_h} \quad \text{for the } z \text{ transform,} \quad (19a)$$

and

$$c_h = (s - r_h) P|_{s=r_h} \text{ for the Laplace transform.} \quad (19b)$$

It is slightly more complicated for repeated roots, but nonetheless quite straightforward (Cadzow 1973).

If a network contains both integrators and fixed time delays, then the resulting unit cohort responses will contain terms in s and terms in e^s. In such cases, there presently are no simple systematic methods for finding the inverse transform. A few specific transforms have been found and are available in the more extensive tables of Laplace transforms (Erdélyi et al. 1954). But in general, the modeler wishing to obtain estimates of a complete solution would be wise to convert the state space to discrete time and either use the z transform or digital simulation.

INTERPRETATIONS OF UNIT COHORT RESPONSES

The unit cohort response of a network model represents expected, or mean behavior of the modeled system as a result of one individual that was part of the input flow or input pool at time zero. In discrete time, as defined in this paper, the value of the unit cohort response of a given flow variable at time τ is the predicted expected number of individuals entering or emerging from the corresponding process at τ. In continuous-time, the value of the unit cohort response of a flow variable at time t is the expected number of individuals per unit time participating in that flow at t, and the unit cohort response of a pool variable (N) at t is the expected number of individuals in the corresponding pool at t. Thus, both in discrete and continuous time, and in spite of the fact that the actual flow or pool itself must be made up of discrete individuals, the unit cohort response generally will take on nonintegral values, representing predicted mean or expected numbers of individuals.

In general, the postulated input flow or pool size will not be specified for a single moment, but will be distributed over time in some fashion. In that case (as long as the model is linear), the resulting response is generated by the convolution of the input distribution and the unit cohort response. Such con-

volutions are carried out most easily when the functions involved are in the forms of z or Laplace transforms (Table 1). Therefore, the analysis of the complete response to a given input function can be accomplished in a straightforward manner if both the input function and the unit cohort response can be transformed into ratios of polynomials in z or s; in which case the transform of the convolved functions also will be a ratio of polynomials in z or s and can be inverted to a corresponding function of time through partial-fraction expansion. The class of input functions that transform to polynomial ratios is very large, including impulses, steps, ramps, exponentials, sinusoids, and all responses to such functions by linear, time invariant networks that do not contain both integrators and fixed time delays.

ROOTS OF THE CHARACTERISTIC FUNCTION

The determination and interpretation of the significant roots (zeros) of the characteristic function of the system (i.e., the denominator on the right-hand side of Eq. 7) can, in itself, be a final outcome of linear flow graph analysis. In networks that do not contain both integrators and fixed time delays, the function will be a polynomial in s or z. Only in very simple models, however, can one expect the degree of this polynomial to be sufficiently low to allow analytical solution for its roots (i.e., solutions that can carry the network's scale factors in literal form as well as in the form of specific numerical values). More generally, the solution for the roots of the polynomial can be expected to require numerical methods, which are widely available (e.g., Newton's method for real roots and Bairstow's method for complex roots, Salvadori and Baron 1952, Young and Gregory 1972). As long as one is forced to use numerical methods for root determination, there is very little difference in difficulty between polynomials and transcendental functions, such as those containing terms in s and terms in e^s. Thus, if he or she is interested in the roots of the characteristic function, a modeler should feel free to employ networks containing both integrators and fixed time delays.

The largest real root of the characteristic function can be interpreted directly in terms of the dominant population growth pattern predicted by the model, being either the exponential coefficient of the dominant exponential growth term or the common ratio of the dominant geometric growth term. The complex roots for both types of transforms as well as the negative real roots for z transforms can be interpreted directly in terms of the frequencies of oscillations or population waves predicted by the model; by comparing these roots with the largest real root, one can deduce the predicted propensity

of the population to sustain the oscillations (Keyfitz 1972).

The interpretations of roots can be used in two directions. If reasonable estimates of the life history parameters are available but overall population dynamics are not, then the root interpretations can be used to deduce estimates of the latter. On the other hand, if one or more life history parameters is in doubt, but overall population dynamics are reasonably well known, then the root interpretation can be used to deduce estimates of the former.

A NUMERICAL EXAMPLE: HERRING-GULL POPULATION

The model of Fig. 3Ac can be used to represent the Herring Gull (*Larus argentatus*) population associated with a given colony, neglecting migration between colonies. For the purpose of generating a numerical example, the following parameter values will be used: $K_1 = 0.4$ (Drury and Smith 1968); $K_2 = 0.35$, $K_3 = 0.6$ (Drost et al. 1961); and $K_4 = 0.94$, expected number of male or female fledglings per adult pair $= 0.5$ (Kadlec and Drury 1968; Kadlec et al. 1969). With these parameter values, the factors of the linear flow graph of Fig. 3Bc take the following forms: $a = 0.4z^{-36}$; $b = 0.611z^{-12}$; $c = 0.35$; $d = 0.6$; $e = 0.376z^{-12}$; $f = 0.94z^{-12}$; and $g = 0.5$. The characteristic function (Table 2) is

$$1 - f - acg - abdg - abeg$$
$$= 1 - 0.94z^{-12} - 0.07z^{-36} - 0.7332z^{-48}$$
$$- 0.0459472z^{-60}. \tag{20}$$

Since the breeding of the entire population is synchronized to within 1 mo of each year, there is no reason to carry a temporal resolution of < 1 yr. One can change the temporal resolution from 1 mo to 1 yr by substituting z^{-1} for z^{-12} in the function. Doing this and then multiplying by z^5, one obtains

$$z^5 - 0.94z^4 - 0.07z^2 - 0.7332z - 0.0459472.$$

Beginning with the assumption that the real root is 1.0 (a very good starting point for z-transform characteristic functions of populations models), six iterations of Newton's method yields the root

$$z_0 = 1.08861615 \tag{21}$$

which is accurate to eight places. Dividing ($z - 1.088161615$) into the characteristic function, one obtains the fourth-degree polynomial

$$z^4 + 0.1486z^3 + 0.1618z^2 + 0.1061z + 0.0422,$$

whose roots are complex and can be found by the quadratic factoring method of Bairstow or by direct analysis. By either method, one obtains the quadratic factors

$$z^2 - 0.4532z + 0.287$$

and

$$z^2 + 0.6018z + 0.147$$

which, in turn, lead directly to the roots

$$z_{1,2} = 0.227 \pm i\,0.486 \tag{22}$$

and

$$z_{3,4} = -0.301 \pm i\,0.238. \tag{23}$$

The real root implies a dominant growth pattern in which the population increases by nearly 9%/yr (giving a predicted population doubling time of between 8 and 9 yr). The complex roots imply the possibility of population waves with periods of ≈ 5.5 years (corresponding to $z_{1,2}$) and 2.5 yr (corresponding to $z_{3,4}$). These waves would be triggered by a transient stimulus to the population. However, according to the magnitudes of the roots, once triggered, the waves would tend to die away rather rapidly. The magnitude of the roots $z_{1,2}$ is 0.536 while that of $z_{3,4}$ is 0.383. The waves should die away geometrically as $(0.536)^T$ and $(0.383)^T$, respectively, where T is the time in years since the disturbance that triggered the waves. Relative to the dominant growth pattern, they will die away even faster (i.e., as $[0.536/1.0886]^T$ and $[0.383/1.0886]^T$, respectively). On the basis of these results, one would predict that the modeled population has little propensity to sustain waves.

In some areas (e.g., the Atlantic coast of North America) where Herring Gull populations are expanding rapidly in the face of increasing resources (e.g., garbage), the population doubling time for some colonies is quite comparable to that predicted here (Kadlec and Drury 1968). On the other hand, in other areas (e.g., the Atlantic coast of Europe), where conditions are more stable, the doubling time is considerably longer (e.g., 20 yr, Harris 1970). The propensity toward wave activity seems to vary considerably from colony to colony, being very low in some, high in others, with wave periods ranging from 2 to 10 or more years (Kadlec and Drury 1968, Drury and Nisbet 1969, Harris 1970), indicating that the values of the parameters of the model should be determined on a colony by colony basis and probably are influenced markedly by ecological context.

COMPARISON WITH LESLIE TYPE MODELS

The standard linear population models (Leslie matrix, renewal equation, von Foerster equation) are compatible with standard, age-specific demographic-type data, which give the expected probabilities of survival and of offspring production as functions of age. The models presented in this paper are compatible with life history data of another type, namely

data concerning underlying natality and mortality processes. The differences and the equivalences between the two classes of models perhaps can best be illustrated by considering the discrete-time versions (i.e., by comparing the Leslie-matrix type model with the z-transform network type model). The characteristic polynomial of a Leslie-matrix model exhibits a single positive term (the term of highest degree) and a negative term for each of the other degrees represented (with the possibility of having every degree from the highest on down to and including zero represented) (see the entry for Fig. 7A in Table 2, and Pielou 1969).

Because each term in this characteristic polynomial includes an independent multiplicative factor, the subdiagonal element of the matrix, an infinite number of Leslie-matrix models, can be constructed to provide any given polynomial of the type described. The same type of characteristic function arises from network models in which all loops touch (i.e., pass through common nodes in the corresponding flow graph) but not from network models with loops that do not touch. Therefore, in principle, any network model in which all loops touch has an infinite number of Leslie-matrix equivalents, in the sense that they provide the same characteristic polynomial; but a network model with any number of nontouching loops in general will have no Leslie-matrix equivalent (in other words, the model simply could not have been formulated in terms of the Leslie matrix).

Since the age profiles of its time delays need not be specified, a discrete-time network model usually does not carry the modeled population's age structure on a time-unit by time-unit basis. Therefore, when Leslie-type equivalents do exist, they will be overspecified (as far as the network model is concerned), and, thus, not unique with respect to age structure. Generally, the simplest Leslie-type equivalent to derive is that in which age structure is ignored altogether, and the natality and survivorship factors are combined to form the elements of the first row, leaving each of the subdiagonal elements equal to one. The row elements of this equivalent are found by the following method: cut the network path representing the flow of new offspring into the population thereby forming two paths, one leading into the network and one leading out of it; determine the flow in the new output path in response to a unit cohort applied to the new input path. In other words, one finds the equivalent Leslie-type model by complete analysis of the unit-cohort response of a modified version of the network model.

Thus, for the types of life history data postulated or given in the examples of this paper, the network method can be used directly, the Leslie method generally cannot. By the same token, although a network model can be used directly for situations in which demographic-type life histories are given or postulated, it offers no advantages over the Leslie-type model (once the simple algorithm for deriving the characteristic polynomial is known), and it has the disadvantage of being considerably less compact (Fig. 7A).

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