A Numerical Model for Tracking Populations through a Time-Dependent Stochastic Network

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ABSTRACT

Units from a population arrive from an external source in a random or fixed pattern at an initial compartment of a D-compartment, linked, network. Once inside the network, individuals move in a statistically independent manner among compartments, finally entering absorbing compartments from which they never depart. A numerical adaptation of the model is described and demonstrated. The model is compared to the MacArthur-Wilson model of island biogeography with respect to differences in statistics of movements that each model is capable of generating. A numerical example is given.

I. INTRODUCTION

Compartmental models are applied widely in epidemiological, health, biological, and management sciences, the mathematical theory of which rests upon ordinary differential equations [8]. Stochastic compartmental models have been applied as well, although limited in application by assumptions of linearity, small numbers of compartments, simplified network topology, exponential residence times of individuals in compartments, and single classes of input populations [2, 6, 11, 12, 14, 17, 18, 21]. Exponentially distributed residence times of individuals in compartments (synonymous with "states" or "nodes") insure Markovian behavior of movements of individuals throughout nonabsorbing compartments (synonymous here with transient compartments,

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transient states or transient nodes) of a linked network of compartments. Individuals' movements throughout transient compartments are usually assumed to be statistically independent, an assumption made here as well. Parameters of behavior of individuals within compartments have traditionally been specified on a compartment-by-compartment basis with no relationships among compartmental parameters. That assumption is not required here.

In this paper, a model is presented in which (independent) movements of individuals inside a network of transient and absorbing compartments are governed by a Markov-renewal process $\{X_n, t_n;\ n = 0, 1, 2, \cdots\}$ with associated semi-Markov process $\{X(t);\ t > 0\}$ where $X(t)$ is the state of the process (location of an individual in the network) at its most recent change of state. States of $\{X_n, t_n\}$ are in one-to-one correspondence with network nodes (i.e., compartments). A numerical adaptation of this model was developed and implemented on the Macintosh platform [21]. A demonstration of the numerical model was made by Snyder to island biogeography [1, 9, 10]. In that application, Snyder [21] demonstrated several generalizations of the earlier MacArthur-Wilson model.

1. THE STOCHASTIC COMPARTMENTAL MODEL

Let $\{\pi(D);\ D = 2, 3, \cdots\}$ denote a family of D-node stochastic compartmental networks in which independent movements of individuals inside $\pi(D)$ are controlled by a D-state, time-invariant, Markov-renewal process $\{X_n, t_n;\ n = 0, 1, 2, \cdots\}$ with associated semi-Markov process $\{X(t);\ t > 0\}$ where $X(t)$ is the state of the process at its most recent change of state. States of $\{X_n, t_n\}$ are in one-to-one correspondence with nodes (compartments) of $\pi(D)$. Individual arrivals to $\pi(D)$ are assumed to enter at a single initial compartment of entry and all absorbing compartments (sinks) are assumed to be accessible from the initial compartment of entry into $\pi(D)$. The underlying embedded Markov chain $\{X_n;\ n = 0, 1, 2, \cdots\}$ of the Markov-renewal process is characterized by a stochastic, absorbing transition matrix $P = (p_{jk})$ containing at least one transient state corresponding to the initial compartment of entry for individuals entering $\pi(D)$ and at least one absorbing state. Let $P^0 = (p_1, \cdots, p_D)$ denote an initial state vector for the process so that $p_j = P(X_0 = j) = P(X(0+) = j)(j = 1, \cdots, D)$.

Let $W(t) = (w_{jk}(t))$ denote a matrix of conditional residence time distribution functions for a typical individual in any transient compartment of $\pi(D)$. $w_{jk}(t)$ is the conditional probability that residence time of an individual in compartment j, given that it next enters compartment k, does not exceed $t (k \neq j)$. An individual is assumed to move to a different compartment once it leaves a transient compartment.

Let $F(t) = (f_{jk}(t))$ denote a stochastic matrix of interval transition probability functions. Assuming time invariance, the conditional probability that $X(t) = k$, given that $X(z) = j$ $(0 \leqslant z < t < \infty)$ is $f_{jk}(t - z)$.

The unconditional probabilities $P(X(t) = k)(k = 1, \cdots, D)$ that the semi-Markov process is in state k at time $t > 0$ is related to the interval transition probabilities through the relations

$$P(X(t) = k) = \sum_{j=1}^{D} P[X(t) = k \mid X(0+) = j] \times P(X(0+) = j)$$

$$= f_{1k}(t) \times p_0 + \cdots + f_{Dk}(t) \times p_D \qquad (k = 1, \cdots, D).$$

The time rate of change of $P(X(t) = k)$ is therefore

$$\frac{dP}{dt}[X(t) = k] = \sum_{j=1}^{D} \dot{f}_{jk}(t) \times p_j \qquad (k = 1, \cdots, D),$$

where $\dot{f}_{jk}(t)$ denotes first derivative of $f_{jk}(t)$ with respect to t.

Thus, for instance, if $P^0 = (1, 0, \cdots, 0)$ then

$$\frac{dP}{dt}[X(t) = k] = \dot{f}_{1k}(t).$$

Solution for $f_{1k}(t)$ in this instance is equivalent to solving for the unconditional probability that the semi-Markov process is in state k at time t. The above relations show the central role played by the interval transition probability functions in computing the unconditional probabilities

$$P(X(t) = k) \qquad (k = 1, \cdots, D; t > 0).$$

Probabilities $P(X(t) = k)$ have the equivalent interpretation in terms of individuals and compartments.

Let $Q(t) = (q_{jk}(t))$ denote a matrix of joint probabilities defined as

$$q_{jk}(t) = Pr(X_{n+1} = k, t_{n+1} - t_n \leqslant t \mid X_n = j; j \neq k),$$

where index j denotes a transient state (node), and index k denotes either a transient or absorbing state.

Probabilities $w_{jk}(t)$, $q_{jk}(t)$, and p_{jk} are related as follows:

$$w_{jk}(t) = Pr(t_{n+1} - t_n \leqq t \mid X_n = j,\ X_{n+1} = k;\ j \neq k)$$

for transient states j from which:

$$w_{jk}(t) = q_{jk}(t)/p_{jk} \qquad (p_{jk} > 0),$$

where

$$p_{jk} = \lim_{t\to\infty} q_{jk}(t) = \Pr(X_{n+1} = k \mid X_n = j;\ j \neq k).$$

Interval transition probability functions $f_{jk}(t)$ can, in the general case, only be approximated. Exceptions occur in cases where compartments are connected in series only, and in certain slightly more complex network topologies. A more detailed definition of elements of P, Q, W, and F that includes all special cases is given in Snyder [21] and Medhi [13].

The matrix P has the form

$$P = \begin{bmatrix} I & O \\ A & N \end{bmatrix},$$

where the sxs block N contains transfer probabilities among transient states; the $sx\ (n - s)$ block A contains transfer probabilities from transient into absorbing states, the $(n - s)\ xs$ block O contains zeros, and the $(n - s) \times (n - s)$ block I is a unit diagonal submatrix. The mean residence time of a typical individual in the set of transient states, given initial entry into the single initial state 1 is

$$\mu = \sum_{i=s+1}^{n} \mu_{1i} p_{1i} \sum_{j=1}^{s} m_{1j} \sum_{i=s+1}^{n} \mu_{ji} p_{ji}, \tag{1}$$

where m_{ij} is the i,jth element in the sxs matrix, $[m_{ij}] = [I - N]^{-1}$, μ_{ji} is the mean of the conditional residence time c.d.f. $w_{ji}(t)$ (in the jth row and ith column of $W(t)$), and p_{ji} is the element in the jth row and ith column of P.

Let $H(z)$ denote the residence time c.d.f. of a typical individual in the set of all transient compartments, having once entered initial compartment 1 from a source outside the network. $H(z)$ is also known as the first passage time c.d.f. of the (time-invariant) Markov-renewal process into an absorbing state, given that its initial state is node 1. The mean of $H(z)$ is known from theory to be given the right side of (1). When the external process of arriving individuals is Poisson distributed with nonnegative intensity $a(t)$ the c.d.f. of total count of individuals in the subset of all transient compartments at any time $t(t > 0)$ is known to be Poisson distributed with mean equal to

$$\int_0^t a(z)(1 - H(t - z))\, dz,$$

where the network of transient compartments is assumed to contain no individuals at initial time $t = 0$. When $a(t)$ is a constant, say a, the mean number of individuals in the subset of all transient compartments is

$$a \sum_{j=1}^{s} m_{1j} \sum_{i=1}^{D} \mu_{ji} p_{ji}.$$

Other relationships are known and can be referenced in texts on applied stochastic processes [13]. Allen and Matis [2] have derived formulae for the mean residence time of individuals in transient compartments when the process describing movements of individuals among compartments is Markovian.

Differences in the information content of deterministic and stochastic versions of finite-state, continuous-time compartmental models are significant. Allen and Matis [2] emphasized mean residence times of individuals in transient compartments as important characteristics obtainable from Markovian models. Other information obtainable from stochastic compartmental models is given in literature [17, 22] including residence time c.d.f. of an individual in a compartment (also called the survivor function for a given state), mean number of transitions of an individual among compartments in a given time period, probabilities of an individual transferring from a transient compartment to any other compartment in a time period, c.d.f.'s of magnitudes of net balances of individuals in compartments at fixed times, c.d.f.'s of lengths of times required for individuals to move between any two compartments, and c.d.f.'s of number of times individuals recycle among transient compartments. In stochastic compartmental models, effects of randomness are accounted for in arrival patterns of individuals from external sources, lengths of residence times of individuals in compartments, and rules for routing individuals among compartments.

All definitions and relationships given above exist in literature of stochastic compartmental modelling and applied stochastic process theory. They are structural only, requiring for numerical implementation in case studies more detailed information about how individuals make choices when transferring into and out of compartments, whether and how compartments interact when individuals transfer among compartments, compartmental residence time parameters, and arrival statistics for individuals entering a network of compartments from external sources, Information must be supplied at two levels of detail: (a) nonnumerical specification of distributions, parameters, and routing rules in terms of which structural parameters defined above can be written, and (b) assignment of numerical values of parameters and operational rules from which full numerical models can be constructed. These information requirements can only be satisfied on a case-by-case basis.

3. CASE STUDY APPLICATION TO ISLAND BIOGEOGRAPHY

In an application of stochastic compartmental modelling motivated by the MacArthur-Wilson ecological theory of island biogeography [3–5, 10], Snyder [21] created a numerical model of movements of a population through a linked, open network of compartments based on theory outlined above. A compartment may correspond to a biophysical condition of an individual, a biophysical habitat, or a geographical area. Absorbing compartments may refer to any habitats, or biophysical conditions from which individuals, once having entered, never emerge such as a life stage including death. If a compartment is not absorbing, it is called transient. The numerical model was implemented on the Macintosh platform in three versions. It is interactive, querying the user for information needed to make computations. An editor is included so that modifications of input may be made either before or after a run. Computations include the P and $W(t)$ matrices for networks containing up to seventy-five compartments. Computational problems encountered in model creation that required resolution included (a) round-off errors, (b) overflow, (c) underflow, (d) raising real numbers to integer powers, and (e) computing factorials for large n. Log-gamma functions and Stirling's approximations are used to store and compute factorials of n that exceed 300.

The following distributions were specified governing residence times of individuals in transient compartments. For every transient compartment j let V_{jk} denote a γ distributed random variable with mean κ/λ and variance κ/λ^2 ($\kappa = 1, 2, \cdots$; $\lambda > 0$) where k denotes a compartment into which an individual can transfer directly from compartment j. If k is the only compartment to which j is linked then the residence time of an individual in compartment j is V_{jk} (parameters λ and κ are specific to the ordered pair of indices (j, k), i.e., $(\lambda, \kappa) \equiv (\lambda_{jk}, \kappa_{jk})$). Denoting the c.d.f. of V_{jk} as $G_{jk}(t)$, we have

$$1 - G_{jk}(t) = \frac{e^{-\lambda_{jk}t}}{(\kappa_{jk}-1)!}\Big[(\lambda_{jk}t)^{\kappa_{jk}-1} + (\kappa_{jk}-1)(\lambda_{jk}t)^{\kappa_{jk}-2} + \cdots + (\kappa_{jk}-1)!\Big].$$

If two or more compartments are directly accessible from transient node j (say the d compartments $1_j, \cdots, d_j$), then these d compartments may be thought of as directly competing for an individual as it completes its residence time in transient compartment j (perhaps with assistance from compartment j). The $2d$ parameters of the Gamma distributed random variables $V_{j1_j}, \cdots, V_{jd_j}$ may be further constrained by sets of relationships beyond the requirements that each κ must be a positive integer and each λ must be positive and real. For instance, differences between physical conditions in two compartments may dictate that one mean be larger than another. The $V_{j1_j}, \cdots, V_{jd_j}$ are all assumed to be statistically independent but that assumption does not disallow constraining relationships among the parameter sets $(\lambda_{j1_j}, \cdots, \lambda_{jd_j}, \kappa_{j1_j}, \cdots, \kappa_{jd_j})$. As suggested above, such constraints may be the result of biophysical or other real connections between individuals or populations. If more than one set of constraints affects a given group of parameters, it may be impossible to find exact solutions to the constraining relationships in which case some type of optimizing procedure may be needed to find approximate solutions for the parameters.

Gamma distributions are chosen to describe the random variables V_{jk} for two reasons: Being two parameter c.d.f.'s they are capable of simulating a variety of residence time distributions, even including approximations to constant residence times. Second, a γ distributed random variable is decomposable as a sum of exponentially distributed random variables so that total time of residence of an individual in a transient compartment can be broken down into stages, the residence time in any given stage being exponentially distributed. In this way, a semi-Markov process describing individuals movements through transient compartments can be reduced to a simple Markovian description, but at the expense of increasing the number of states of the process. The corresponding "compartments" would be hypothetical only. A major advantage of expanding the state description of the controlling stochastic process to a Markovian process is realized in the computation of the $F(t)$ matrix.

For absorbing compartments j, there are no random variables defined that describe residence times.

If a compartment k is the only one to which transient compartment is directly linked then the conditional residence time distribution $w_{jk}(t)$ is identical to $G_{jk}(t)$. The unconditional residence time probability for transient compartment j is $\Sigma_k\, p_{jk} \cdot q_{jk}(t)$.

Individuals in this model are assumed to move throughout transient compartments in a manner statistically independent of each other, although their movements may be functionally linked as indicated above.

An important exception to the statistical independence assumption occurs in population dynamics when individuals move from place to place in groups or move from one biophysical condition to another en masse. In such instances the model is modified to interpret an individual to be an individual group of some fixed or variable size. Counts of individuals in compartments are then computed as functions of counts of numbers of individual groups in each compartment. Groups, then, are assumed to move statistically independent of each other.

4. COMPUTATION OF ELEMENTS OF MATRIX $Q(t)$

Elements $q_{jk}(t)$ of $Q(t)$ are computed for all transient nodes j (compartments j) by decomposing $q_{jk}(t)$ into a product

$q_{jk}(t)$ = Pr[time of residence of a unit having just arrived in node j does not exceed t and its next transfer is into node k, $k \in (1_j, \cdots, d_j)$]

= Pr[time of residence of a unit having just arrived in node j does not exceed t, given its next transfer is into a node in the set with indices $(1_j, 2_j, \cdots, d_j)$]

× Pr[the unit's next transfer from node j is into node k, given that k is an index in the set $(1_j, \cdots, d_j)$]

$$= \Pr[\min(V_{j1_j}, \cdots, V_{jd_j} \leqq t)] \times \Pr[V_{jk} < \min(V_{j1_j}, \cdots, V_{j,k-1}, V_{j,k+1}, \cdots, V_{jd_j})]. \qquad (1)$$

The first term on the right side of (1), the unconditional probability of an individual residing in transient node j during any sojourn for at most t time units is most easily computed by first recognizing that the event that the smallest of the d_j random variables $V_{j1_j}, \cdots, V_{jd_j}$ assumes a value not exceeding t in magnitude is the logical complement of the event that all d_j of the V_{jk} random variables assume values, independently, which are greater than t.

Therefore, the first term is equal to

$$1 - Pr\left[V_{j1_j} > t, \cdots, V_{jd_j} > t\right] = 1 - \prod_{\alpha = 1j}^{d_j} P \qquad (V_{j\alpha} > t)$$

$$= 1 - \prod_{\alpha = 1j}^{d_j} \left(1 - G_{j\alpha}(t)\right).$$

The second term on the right side of (1) is evaluated to yield

$$P\left[V_{jk} < \min\left(V_{j1_j}, \cdots, V_{j,k-1}, V_{j,k+1}, \cdots, V_{jd_j}\right)\right]$$

$$= \sum_{i_{1_j}=0}^{\kappa j 1_j - 1} \cdots \sum_{i_{d_j}=0}^{\kappa j d_j - 1} \left[\frac{\left(\kappa_{jk} - 1 + \sum_{m=1_j}^{d_j} i_m\right)!}{\left(\prod_{m=1_j}^{d_j} i_m!\right)\left(k_{jk} - 1\right)!}\right]$$

$$\times \left(\frac{\lambda_{j1_j}}{\lambda}\right)^{i_{1_j}} \times \left(\frac{\lambda_{j2_j}}{\lambda}\right)^{i_{2_j}} \times \cdots \times \left(\frac{\lambda_{jd_j}}{\lambda}\right)^{i_{d_j}} \times \left(\frac{\lambda_{jk}}{\lambda}\right)^{\kappa_{jk}}, \qquad (2)$$

where $\lambda = \lambda_{jk} + \lambda_{j1_j} + \lambda_{j2_j} + \cdots + \lambda_{jd_j}$. The index k is *not* included in any sequence of indices ranging from $j1_j$ to jd_j.

The right side of equation (2) is a multiple sum of multinomial probabilities. As demonstrated, the number of terms depends directly upon network topology (the d_j's), the parameters $\kappa_{j\alpha}$, and indirectly upon the number D of nodes in the network ($1 \leqq d_j < D$, all j). The computation presents no problem for small D, $\kappa_{j\alpha}$, and d_j. As these integer valued parameters increase in magnitude the factorials must eventually be approximated (Stirling's approximation) as a limit is reached on the magnitude of factorials that can be stored as whole numbers in tables. Additionally, the right side of equation (2) may yield extremely small values, leading to loss of significant digits in the result. Roundoff of individual terms is avoided until the final result is reached. Details of numerical calculations of the right side of (2) are given by Snyder [21].

For absorbing nodes j, distributions of $q_{jk}(t)$ are degenerate. For nodes k which are not directly accessible from node j, $q_{jk}(t)$ is defined to be zero for all $t > 0$.

5. COMPUTATION OF ELEMENTS OF P

The relation $p_{jk} = \lim_{t \to \infty} q_{jk}(t)$ yields for transient nodes j

$$p_{jk} = P\left[V_{jk} < \min\left(V_{j1_j}, \cdots, V_{j,k-1}, V_{j,k+1}, \cdots, V_{jd_j}\right)\right]. \tag{3}$$

6. COMPUTATION OF ELEMENTS OF $W(t)$

For transient nodes j we have the relation

$$w_{jk}(t) = Pr\left[t_{n+1} - t_n < t \mid X_n = j, X_{n+1} = k\right]$$

from which we obtain the formula

$$w_{jk}(t) = q_{jk}(t)/p_{jk} \qquad (p_{jk} > 0).$$

Upon substituting, we have for all transient nodes j,

$$w_{jk}(t) = P\left[\min\left(V_{j1_j}, \cdots, V_{jd_j}\right) < t\right]$$

$$= 1 - \prod_{\alpha = 1j}^{d_j} \left(1 - G_{j\alpha}(t)\right). \tag{4}$$

Since in the present instance, $w_{jk}(t)$ is the same for all indices in the index set $(1_j, \cdots, d_j)$ the conditional residence time c.d.f. $w_{jk}(t)$ is also equivalent to $\Sigma_k\, p_{jk} w_{jk}(t)$, the unconditional residence time of an individual in compartment j for a single sojourn.

The mean unconditional time of residence of an individual in transient node j for a single sojourn in node j is therefore $\mu_j = \int_0^\infty (1 - w_{jk}(t))\, dt$ for any compartment k in the set $(1_j, \cdots, d_j)$, or $\mu_j = \mu_{j1_j} = \cdots = \mu_{jd_j}$.

7. COMPUTATION OF ELEMENTS OF $F(t)$

Explicit analytical solutions for interval transition probability functions cannot be obtained in general and in most cases must be numerically approximated. In certain special cases of network linkages consisting of compartments linked in series or simple variations thereof, analytical solutions can be obtained for some residence time c.d.f.'s $w_{jk}(t)$. When the process governing movements of individuals among compartments is strictly Markovian (meaning that all compartment residence time c.d.f.'s are exponential), the form of an exact analytical solution for the $f_{jk}(t)$'s is known. This is because they are the solutions to a linear time-invariant system of first-order differential equations and the solution to that system is well-known, even though numerical solutions usually require approximation. In steady state cases, the $f_{jk}(\infty)$'s can be computed as solutions to a linear system of algebraic equations. One method for approximating the $f_{jk}(t)$'s makes use of powers of the submatrix N (defined above) and is effective when entries of N^r are near zero for small integers r, a condition that depends upon both compartmental linkages and values of the parameters of the $G_{jk}(t)$'s. Snyder's numerical model does not compute interval transition probability functions.

8. NUMERICAL EXAMPLE

Snyder computed numerical examples of P and $W(t)$ matrices for several compartmental networks, including the following case.

A three-node network (Figure 1) consists of initial node 1, node 2, and absorbing node 3, with nodes 1 and 2 being transient. Interpreted in terms of island biogeography theory, node 1 may be a preferred seasonal habitat, node 2 may be a place where an individual resides when not in its preferred habitat, and node 3 represents a biological condition such as non-reproductive or even death.

For transient node 1 parameters of c.d.f.'s in the group $(V_{11_1}, V_{12_1}) \equiv (V_{12}, V_{13})$ are $\lambda_{12} = 2$, $\kappa_{12} = 2$; $\lambda_{13} = 2$, $\kappa_{13} = 2$. For transient node 2, the corresponding group $(V_{21_2}, V_{22_2}) \equiv (V_{21}, V_{23})$ has parameters $\lambda_{21} = 1$, $\kappa_{21} = 2$; $\lambda_{23} = 2$, $\kappa_{23} = 2$.

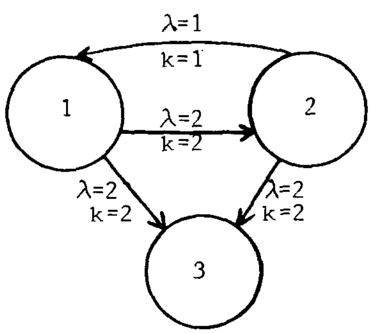

FIG. 1. Three-node compartment model with γ distributed node residence times.

The P matrix is computed from (2) to be

$$P = \begin{bmatrix} 0.000 & 0.500 & 0.500 \\ 0.556 & 0 & 0.444 \\ 0.000 & 0.000 & 1.000 \end{bmatrix}.$$

Rearranged in the block form defined above,

$$P = \begin{bmatrix} I & O \\ A & N \end{bmatrix} = \begin{bmatrix} 1.000 & 0.000 & 0.000 \\ 0.500 & 0 & 0.500 \\ 0.444 & 0.556 & 0 \end{bmatrix}.$$

Powers P^2 and P^4 represented in the given block form are

$$P^2 = \begin{bmatrix} 1.000 & 0.000 & 0.000 \\ 0.722 & 0.278 & 0.000 \\ 0.722 & 0.000 & 0.278 \end{bmatrix}$$

and

$$P^4 = \begin{bmatrix} 1.000 & 0.000 & 0.000 \\ 0.923 & 0.077 & 0.000 \\ 0.923 & 0.000 & 0.077 \end{bmatrix}.$$

After four transitions, starting from state 1, there is more than a 92% chance that the governing semi-Markov process will be in state 3 after four transitions. Restated in terms of population movements among the three-compartment network, after a typical individual initially entering the network in compartment 1 has made four transitions, there is a 92% chance it will be in compartment 3. Higher powers of P produce a block form in which the second and third columns contain entries all of which are approaching zero while the first column contains entries approaching unity.

The $W(t)$ matrix, being a function of calendar time t, is a continuous family of 3 by 3 matrices. For $t = 0$, 1.00, and 3.00:

$$W(0) = \begin{bmatrix} - & 0.000 & 0.000 \\ 0.000 & - & 0.000 \\ - & - & - \end{bmatrix} \text{current node;}$$

$$W(1.00) = \begin{bmatrix} - & 0.835 & 0.835 \\ 0.851 & - & 0.851 \\ - & - & - \end{bmatrix};$$

and

$$W(3.00) = \begin{bmatrix} - & 1.000 & 1.000 \\ 0.999 & - & 0.999 \\ - & - & - \end{bmatrix}.$$

For instance, the probability that a typical individual will have a sojourn time in compartment two for at most 1.00 (residence) time unit is 0.851, increasing to 0.999 when the number of residence time units increase to 3.00. The mean unconditional residence times for an individual in nodes 1 and 2 for a single sojourn can be easily approximated using only $W(0)$, $W(1)$, $W(3)$, and assuming the probabilities in $W(4)$ are all equal to unity. As matrices $W(t)$ for additional time points t become available the approximations increase in accuracy. Using only the above matrices, $\mu_1 = \mu_{12} = \mu_{13}$ is approximated as 1.78 (time units) and $\mu_2 = \mu_{21} = \mu_{23}$ is approximated as 1.78 as well.

To obtain the unconditional probability that an individual in transient node j will transfer next to node k, and its time of residence in node j is at most t time units, the probability $q_{jk}(t)$ is computed (1). For instance,

$$q_{12}(1.00) = p_{12} \times w_{12}(1.00) = 0.500 \times 0.835 = 0.418$$

and

$$Q(1.00) = \begin{bmatrix} 0 & 0.418 & 0.418 \\ 0.473 & 0 & 0.473 \\ - & - & - \end{bmatrix}.$$

Probabilities $q_{3j}(t)$ are undefined since $w_{3j}(t)$ is degenerate. The 2×2 submatrix of transfer probabilities is

$$N = \begin{bmatrix} 0 & 0.500 \\ 0.556 & 0 \end{bmatrix},$$

$$I - N = \begin{bmatrix} 1 & -0.500 \\ -0.556 & 1 \end{bmatrix},$$

and

$$[I - N]^{-1} = \begin{bmatrix} 1.385 & 0.692 \\ 0.770 & 1.385 \end{bmatrix}.$$

The unconditional mean time of residence of a typical individual in the subset of transient compartments, initially entering compartment one according to equation (1) is equal to

$$\mu = m_{11} \times (\mu_{13} \times p_{13}) + m_{12} \times (\mu_{23} \times p_{23})$$

$$= 1.385 \times (1.78 \times 0.500) + 0.692 \times (1.78 \times 0.444)$$

$$= 1.233 + 0.547 = 1.78 \text{ time units.}$$

Under equilibrium conditions the expected number of individuals in the subset of transient compartments is $1.78 \times A$ where A is the long-run mean rate of arrival of individuals into the network from an external source.

In cases where a population of size N is initially in residence in the set of transient compartments with no accumulated residence times in those compartments, and the objective is to analyze movements of those N individuals a vector $(N_1, \cdots, N_s)$ of individuals in each of the s transient compartments is defined $(\Sigma N = N)$ from which analyses of their movements can be obtained using only quantities defined above [19].

As indicated above, a technique that is sometimes useful for computing elements of the matrix $(F(t))$, when the controlling process is semi-Markovian and all random variables V_{jk} are Gamma distributed, is to expand the state description of the semi-Markov process (with corresponding expansion of numbers of compartments) so that the expanded set of V_{jk}'s are individually exponentially distributed. The expanded set of $F_{jk}(t)$'s are then solved as a time-invariant, linear system of differential equations with constant coefficients.

To illustrate, Figure 2 shows an expansion of the three-compartment network into a six-compartment network with connecting linkages. Table 1 shows correspondences between interval transition probabilities. $f_{ij}(t)$ and $f_{ij}^*(t)$ where $f_{ij}^*(t)$ is an element of the matrix $F^*(t)$ of interval transition probabilities corresponding to the six-compartment network. Table 1 assumes that an individual must initially occupy the first-stage of any compartment whenever multiple stages occurs for that compartment. For example, compartment 1 in Figure 1 is expanded to three compartments 1, 2, and 3. The model assumes that an individual may, initially, only occupy compartment (stage) 1 in Figure 2 if it initially occupies compartment 1 in Figure 1. Compartment 3 in Figure 2 can be eliminated by combining it with compartment 2, but only because in this instance the parameters λ_{12}, λ_{13}, and λ_{23} are equal in magnitude.

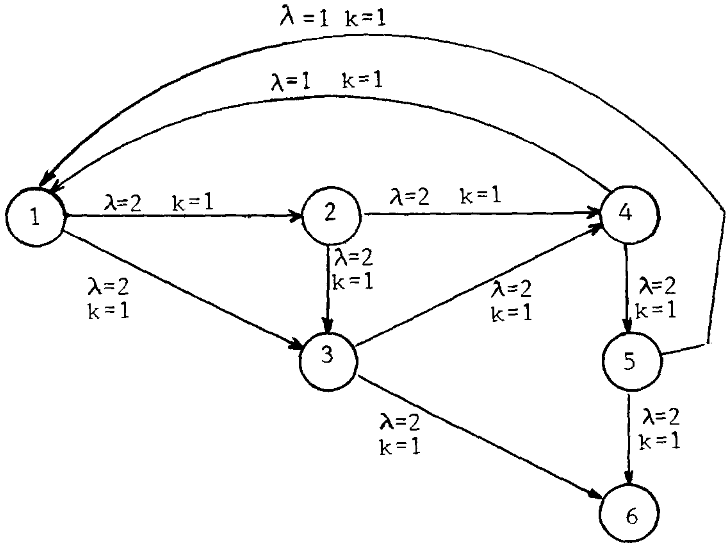

FIG. 2. Six-node compartment model with exponentially distributed node residence times.

Assume in the present example that the six-compartment network is initially empty and individuals arriving from an external source enter compartment 1 only. The unconditional probabilities $P(X(t)=j)$ $(j=1,2,3)$ (Figure 1) can be computed by first computing the $f^*_{1j}(t)$'s and applying Table 1 to obtain the equivalent solution for $f_{1j}(t)=P(X(t)=j)$ $(j=1,2,3)$.

TABLE 1
EQUIVALENCE OF INTERVAL TRANSITION PROBABILITY FUNCTIONS

Three-node network probabilities		Six-node network probabilities
$f_{11}(t)$	=	$f^*_{11}(t)+f^*_{12}(t)+f^*_{13}(t)$
$f_{12}(t)$	=	$f^*_{14}(t)+f^*_{15}(t)$
$f_{13}(t)$	=	$f^*_{16}(t)$
$f_{21}(t)$	=	$f^*_{41}(t)+f^*_{42}(t)+f^*_{43}(t)$
$f_{22}(t)$	=	$f^*_{44}(t)+f^*_{45}(t)$
$f_{23}(t)$	=	$f^*_{46}(t)$

A solution for the linear system

$$\dot{f}_{11}^{*}(t) = -4f_{11}^{*}(t) + f_{14}^{*}(t) + f_{15}^{*}(t)$$

$$\dot{f}_{12}^{*}(t) = -4f_{12}^{*}(t) + 2f_{11}^{*}(t)$$

$$\dot{f}_{13}^{*}(t) = -4f_{13}^{*}(t) + 2f_{11}^{*}(t) + 2f_{12}^{*}(t)$$

$$\dot{f}_{14}^{*}(t) = -3f_{14}^{*}(t) + 2f_{12}^{*}(t) + 2f_{13}^{*}(t)$$

$$\dot{f}_{15}^{*}(t) = -3f_{15}^{*}(t) + 2f_{14}^{*}(t)$$

$$\dot{f}_{16}^{*}(t) = 2f_{15}^{*}(t) + 2f_{13}^{*}(t)$$

$$f_{11}^{*}(t) + f_{12}^{*}(t) + f_{13}^{*}(t) + f_{14}^{*}(t) + f_{15}^{*}(t) + f_{16}^{*}(t) = 1;$$

$$f_{1j}^{*}(t) \geqq 0; \qquad f_{11}^{*}(0+) = 1; \qquad f_{1j}^{*}(0+) = 0 \qquad (j = 2, \cdots, 6).$$

for the $f_{1j}^{*}(t)$'s gives the solution (from Table 1) for the $f_{1j}(t)$'s and hence the unconditional probabilities $P(X(t) = j)$ $(j = 1, 2, 3)$.

Table 2 shows a solution to the above system obtained by numerical integration. Table 3 shows the solution for the corresponding interval transition probabilities associated with the three-compartment network. Time points at which probabilities are computed were selected to show time intervals within which interval transition probability functions peak.

The mean and variance of the c.d.f. of the number of individuals in each compartment at any time t can now be computed, given sufficient informa-

TABLE 2

INTERVAL TRANSITION PROBABILITIES FOR THE SIX-COMPARTMENT MODEL

t	$f_{11}^{*}(t)$	$f_{12}^{*}(t)$	$f_{13}^{*}(t)$	$f_{14}^{*}(t)$	$f_{15}^{*}(t)$	$f_{16}^{*}(t)$
0	1	0	0	0	0	0
0.10	0.667	0.139	0.151	0.027	0.001	0.015
0.25	0.370	0.189	0.235	0.110	0.018	0.078
0.50	0.167	0.144	0.214	0.194	0.066	0.215
0.75	0.106	0.092	0.154	0.195	0.102	0.351
1.00	0.084	0.063	0.109	0.163	0.111	0.470
1.25	0.070	0.047	0.081	0.128	0.103	0.571
2.00	0.038	0.024	0.040	0.062	0.058	0.778

TABLE 3
INTERVAL TRANSITION PROBABILITIES FOR THE THREE-COMPARTMENT MODEL

t	$f_{11}(t)$	$f_{12}(t)$	$f_{13}(t)$
0	1	0	0
0.10	0.957	0.028	0.015
0.25	0.794	0.128	0.078
0.50	0.525	0.260	0.215
0.75	0.352	0.297	0.351
1.00	0.256	0.274	0.470
1.25	0.198	0.231	0.571
2.00	0.102	0.120	0.778

tion about the statistics of the arrival process of individuals from an external source [20]. When individuals arrive in a random (Poisson) stream with intensity $a(t)(a(t) > 0;\ t > 0)$ at initial compartment 1, the number of individuals in each compartment j at any time $t > 0$ is Poisson distributed with mean equal to

$$\int_0^t a(z) f_{1j}(t - z)\, dz$$

assuming no individuals are present in the network at initial time $t = 0$. Using the numerical parameter values given above the process $\{X(t)\}$ is in virtually a steady state after only two time units have elapsed. Thus, solving the more simplified system of algebraic equations representing steady state conditions would have produced constant compartment residence probabilities that represent rather accurately the transient model probabilities for $t > 2.00$.

9. COMPARISONS TO THE MACARTHUR-WILSON MODEL

MacArthur and Wilson [10] assumed the deterministic relationship

$$\frac{dn}{dt} = I(n) - E(n),$$

where $I(n)$ is the (density-dependent) immigration rate for species onto an island from an infinite mainland source, $E(n)$ is the extinction rate of species on the island, and $n(t)$ is the number of species on the island at time $t > 0$.

Both $I(n)$ and $E(n)$ were assigned parametric forms in which the immigration rate decreased linearly as n increased until it reached zero at a preset value of n. Similarly, the extinction rate increased linearly with increasing n until n reached a preset level, whereupon it became constant. MacArthur and Wilson [10] provided supporting evidence for this model. Later, other workers parameterized the immigration rate as a decreasing function of distance from the mainland source to the island, and parameterized the extinction rate as a decreasing function of island size.

When compared to the model that Snyder used as a basis for his numerical adaptation, several important differences stand out. The MacArthur–Wilson model (referred to as the M-W model) contains a single compartment whereas the Snyder model (referred to as the S-model) is programmed to accept up to 75 compartments linked arbitrarily. For instance, the three-compartment model illustrated above can be interpreted in different ways. The second transient compartment may reflect a second island onto which an individual may immigrate periodically before reimmigration back to the first. It may also represent another mainland source to which indivduals migrate after they have once immigrated onto the island. Although the numerical parameters used in the illustration do not suggest it, the second transient compartment may also reflect a biophysical condition on the island occurring and re-occurring randomly in time that changes habitat conditions sufficiently to cause changes in the rates of migration off the island, whether it be back to the source or to the absorbing compartment. Compartment 3 in the S-model provides an ongoing tally of individuals that have migrated into compartment 1 and subsequently departed, never to return.

The M-W model does not provide for randomness in arrival rates or residence times on the island, contrary to the S-model. Patterson [20] developed formulae for computing means and variances of population sizes in individual compartments for three different immigration processes into compartment 1. Those formulae are not demonstrated in this paper. Whereas the M-W model later included distance and area parameters, the S-model did not, although those parameters could easily be incorporated, even for every transient compartment if distances and areas are relevant. In applications to model simulations where animal populations require corridors of certain dimensions for successful migration between habitats, the corridors themselves are represented by compartments having parametric specifications in terms of geometry of biophysical conditions [21] needed by those populations.

As the M-W model contains no provision for statistically variable lengths of times in residence on the island compartment, there is no well-defined mean time of residence of individuals or species on the island, in contrast to the S-model. However, Allen and Matis [2] and others have shown that the solution to the deterministic M-W model (and its deterministic linear, first-order generalizations) under certain conditions is equivalent to the solution for the mean times of residence of individuals in compartments of networks where movements among compartments are governed by Markov processes.

Other statistics describing movements of individuals or populations among compartments that are well-defined for the stochastic model are nonexistent for the deterministic model. For instance, the mean number of times an individual reenters a certain habitat during a period may be a useful statistic for population managers and can be computed provided sufficient data are available. That statistic is not defined for the deterministic model.

10. CONCLUSION

The Snyder [21] numerical implementation of a linear, stochastic compartmental model containing up to 75 compartments, linked arbitrarily, is a contribution to the tool kit for analyzing population movements through a network of corridor-linked habitats. It computes two key matrices that are needed for evaluating and comparing different networks. From these two matrices, other statistics can be computed that are potentially useful. This model is so far the most mathematically sophisticated tool the authors have found in literature of numerical analysis of stochastic compartmental models. That alone does not mean that the model is necessarily going to be relevant to any particular study of patterns of movements of naturally occurring populations. The problem of model specification in a particular case is not addressed in this paper—only the problem of model analysis and what can be computed with an appropriate model once it is specified. Stochastic compartmental models seem to be an obvious tool for analyzing population behavior and movements that exhibit random fluctuations over time.

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