0) > 0. Then $P(B, t) = 1$ for $t = 1, 2, \ldots$ and the theory of stable populations (the Perron–Frobenius theory of primitive matrices in demographic disguise) guarantees that

$$\lim_{t \to \infty} \frac{X_i(BB, t)}{X(t)} = y_i,$$

(3.9)

$$\lim_{t \to \infty} \frac{X(t)}{\rho^t} = \text{constant}, \qquad i = 1, 2,$$

where $\rho > 0$ is the eigenvalue of $L(BB)$ of maximal modulus, and y is the corresponding eigenvector, with positive elements y_1 and y_2 normalized so that $y_1 + y_2 = 1$. Asymptotically the absolute numbers of young and old and the total population size change exponentially, all at the same rate.

Here the key point is that the equilibrial fractions y_1 and y_2 of young and old depend only on $L(BB)$ and are independent of the initial demographic composition of the population (provided the initial population is not zero).

What happens when all the parameters of the full model are nonzero? It appears that nobody knows. In numerical simulations that allowed the Leslie matrices $L(g, t)$ to vary randomly in time, Orzack (1985, page 559) assumed that the model "represents an ergodic process, [so that] numerical analysis consisted of examining the long-run behavior of a single sample path of the process." However, it is clear from the genetic submodel that, even with constant Leslie matrices, the model may not be ergodic in Orzack's sense, in that the long-run behavior may depend on initial conditions. My own numerical calculations of the full model with time-invariant parameters show that sometimes the asymptotic composition of the population depends on the initial conditions, and sometimes is independent of initial conditions. Still other forms of behavior are not yet excluded. Specifying the regions of the parameter space that give the various forms of behavior seems to be a challenging task.

Small-population versions of this model would describe the production and the pairing of gametes and the survival of young as stochastic processes. Similar questions arise, in addition to the problem of characterizing the probabilities of extinction.

Comment

Peter Donnelly

What a pleasure it is to see outlined one of the principal goals in applied probability, the elucidation of the *structure* common to a range of models that enjoy certain basic properties, followed by an exhilarating tour through that structure in the case in which the basic property is that of branching.

The application of these models in the context of genetics serves several purposes. On one level, it broadens our understanding of evolution, in this case through the illumination of a collection of conditions that are consistent with the molecular clock hypothesis. More generally, the contrast between the structure of the branching process models and that of more traditional population genetics models highlights the features of the latter which are fundamental consequences of the correlations in offspring numbers that arise through constraints on total population sizes.

THE STRUCTURE OF GENETICS MODELS

In the neutral case, the structure of population genetics models is now well understood. In a population of fixed size N, which evolves in nonoverlapping generations, we could describe a specific model for the way in which the population reproduces by randomly labeling the individuals in a particular generation and specifying the joint distribution of the random variables $\nu_1, \nu_2, \ldots, \nu_N$, where ν_i is the number of offspring born to the ith individual. The random variables $\{\nu_i\}$ will be exchangeable, and

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