ON LOTKA–VOLTERRA PREDATOR PREY MODELS

L. BILLARD*, *Florida State University*

Abstract

Ever since Lotka (1925) and Volterra (1926), (1931) first considered mathematical formulations for prey–predator processes, the resultant equations have resisted attempts to solve them. However, over the intervening 50 years, standard techniques have allowed a few isolated results to be obtained for some simplified versions of the original process, but the classical equations for the stochastic model have remained unsolved. We give here solutions to the classical process for the case in which interactions occur over a sufficiently short period of time that no births occur. The technique used is one recently developed by Severo (1969a), (1969b), (1971). The approach can be easily generalised to allow solution for the case in which births do occur, as well as for the simplified versions of the original process.

LOTKA–VOLTERRA PREY-PREDATOR MODELS; STATE PROBABILITIES; STOCHASTIC MODEL

1. Introduction

Lotka (1925) and Volterra (1926), (1931) first established mathematical equations governing behavior between two competing species. They assumed that the number of each species varied in a deterministic manner as represented by some differential equation. When two or more species are present, the interactions assumed are such that the resultant models are difficult to solve even in a deterministic approach. In a stochastic approach, we assume that the interaction between species is a random process so that the sizes of the species are random variables with some probability distribution. The mathematical equations associated with these stochastic models are usually non-linear partial differential equations which, while solvable in a few special cases, have generally defied attempts to find useful explicit solutions.

There have been numerous models describing interaction between species, for example, Bartlett (1957), (1960), Becker (1970), Leslie (1948), Leslie and Gower (1958), (1960), Bartlett, Leslie and Gower (1960), Neyman, Park and Scott (1956), Mertz and Davies (1968), Puri (1975) and Weiss (1963). In many instances the models adopted are modifications of the basic Lotka–Volterra models.

375

Whilst some of the modifications are made to better suit the investigator's view of reality for his particular species, many are made in an attempt to find a model which is more tractable mathematically and thus hopefully will provide some insight into the original Lotka–Volterra processes. Even then many of these earlier results deal with deterministic cases with results for the corresponding stochastic models being largely confined to simulation studies. The few theoretical results that are available are frequently isolated results specific to a particular model. Thus as a generalisation, the standard or classical techniques have proved unfruitful in the search for complete solutions. In particular, they have proved unsuccessful in finding the stochastic solution to the all important classical Lotka–Volterra models.

Recently, recursion techniques have been developed by Severo (1969a), (1969b), (1971) for solving any lower-triangular system of differential-difference equations. Of particular importance to us here is that these techniques can indeed be used to establish complete solutions for the Lotka–Volterra models (as well as all the other models mentioned above). Our purpose then is to indicate how the Severo technique can be implemented and thence to provide the solution for the state probabilities for the Lotka–Volterra model governing the prey–predator interaction process in which the species may die but in which no birth occurs in either species. The other models are solved similarly. More complete details of the requirements for his technique and how it operates can be found in the Severo references cited.

2. Lotka–Volterra model

Let $X_1(t)$ be the size of the prey species and $X_2(t)$ the size of the predator species at time t. Let $X(t) = \{X_2(t), X_1(t)\}$ have realisation $x = (x_2, x_1)$ taking values in the space

$$A = \{0 \leq x_i \leq N_i, i = 1, 2\}$$

where $N_i = X_i(0)$, $i = 1, 2$ is the initial size of the prey and predator species, respectively. Let $e_2 = (1, 0)$ and $e_1 = (0, 1)$. Losses occur in the prey species due to predation but the predator species itself suffers losses by the usual natural attrition. Thus, assuming mixing is homogeneous and that two or more transitions occur in the interval $(t, t + h)$ with probability $o(h)$, the infinitesimal transition probabilities in $(t, t + h)$ are

(1)
$$\Pr(x + e_1 \to x) = \mu_1(x_1 + 1)x_2 h + o(h)$$
$$\Pr(x + e_2 \to x) = \mu_2(x_2 + 1)h + o(h)$$
$$\Pr(x \to x) = 1 - x_2(\mu_1 x_1 + \mu_2)h + o(h).$$

Writing

$$q(\boldsymbol{x}; t) = \Pr\{\boldsymbol{X}(t) = \boldsymbol{x} \mid \boldsymbol{X}(0) = \boldsymbol{x}_0\},$$

the Chapman–Kolmogorov equations are

(2)
$$\frac{d}{dt} q(\boldsymbol{x}; t) = -x_2(\mu_1 x_1 + \mu_2) q(\boldsymbol{x}; t) + \mu_1(x_1 + 1) x_2 q(\boldsymbol{x} + \boldsymbol{e}_1; t)$$
$$+ \mu_2(x_2 + 1) q(\boldsymbol{x} + \boldsymbol{e}_2; t), \qquad \boldsymbol{x} \in A$$

where $q(\boldsymbol{x}; t) \equiv 0$ whenever $\boldsymbol{x}$ is not in A.

The most frequently used procedure at this point has been to derive the corresponding partial differential equation for the moment (or probability) generating function. Unfortunately these equations are frequently non-linear and apparently mathematically intractable. The Severo technique is to continue working with the differential-difference equation (2).

Following Severo ((1969a), Section 3), we define a unique counting coordinate $s = s(\boldsymbol{x})$ to each point $\boldsymbol{x} \in A$ as

(3)
$$s = s(\boldsymbol{x}) = (N_1 + 1)(N_2 + 1) - x_1 - (N_1 + 1)x_2.$$

Likewise, we find

$$s(\boldsymbol{x} + \boldsymbol{e}_i) = s(\boldsymbol{x}) - h_i, \qquad i = 1, 2$$

where

$$h_1 = 1, \quad h_2 = N_1 + 1.$$

Hence, writing

$$z_s(t) = q(\boldsymbol{x}; t),$$

the equations (2) become

$$\frac{d}{dt} z_s(t) = -x_2(\mu_1 x_1 + \mu_2) z_s(t) + \mu_1(x_1 + 1) x_2 \varepsilon (N_1 - x_1 - 1) z_{s-1}(t)$$

$$+ \mu_2(x_2 + 1) \varepsilon (N_2 - x_2 - 1) z_{s-N_1-1}(t), \qquad s = 1, \cdots, (N_1 + 1)(N_2 + 1)$$

where $\varepsilon(y) = 1$ for $y \geqq 0$ and $\varepsilon(y) = 0$ for $y < 0$. In matrix form

(4)
$$\frac{d}{dt} \boldsymbol{z}(t) = \boldsymbol{B} \boldsymbol{z}(t)$$

where the matrix of coefficients $\boldsymbol{B}$ is clearly lower-triangular.

The solution to Equation (4) is represented by

$$\boldsymbol{z}(t) = \boldsymbol{C} \boldsymbol{e}(t)$$

where $\boldsymbol{e}(t)$ has elements $\exp(b_i t)$ with b_i being the ith diagonal element of $\boldsymbol{B}$. The elements of $\boldsymbol{C}$ are found from the recursion theorem of Severo ((1969a), Theorem 1).

The derivation of these elements is greatly facilitated if the B matrix is partitioned as

$$B = (B_{lm}), \qquad l, m = 1, \cdots, N_2 + 1$$

where

$$B_{lm} = (b_{lm}(k, w)), \qquad k, w = 1, \cdots, N_1 + 1.$$

From Equation (2), we see that

(5) $\qquad b_{ll}(k, w) = \begin{cases} -(N_2 - l + 1)[\mu_1(N_1 - k + 1) + \mu_2], & w = k \\[2mm] (N_2 - l + 1)\mu_1(N_1 - k + 2), & w = k - 1. \end{cases}$

$$b_{l,l-1}(k, w) = \mu_2(N_2 - l + 2), \qquad w = k.$$

All other elements of B are zero. The matrix C is partitioned similarly so that it has elements

$$C = (c_{lm}(k, w)), \qquad \begin{aligned} l, m &= 1, \cdots, N_2 + 1 \\ k, w &= 1, \cdots, N_1 + 1. \end{aligned}$$

We then have the following result.

Theorem.   For the prey–predator process with transition probabilities given by (2) and parameter values such that the matrix C is independent of t, the elements of C are given by: when $l > m$, $k > w$,

(6) $\qquad c_{lm}(k, w) = \dfrac{\mu_1^{k-w}\mu_2^{l-m}N_1! \, N_2! \, A_{mw}}{(N_1 - k + 1)! \, (N_2 - l + 1)! \, Q(0)} \prod_{v=1}^{k-w} V(v)$

where

$$V(v) = \sum_{\alpha_v = m}^{\alpha_{v+1}} (N_2 - \alpha_v + 1)/Q(v)$$

with

$$Q(v) = \prod_{\beta_v = \alpha_v}^{\alpha_{v+1}} \{-\mu_1[(\beta_v - m)(N_1 - v + w - 1) + v(N_2 - m + 1)] - (\beta_v - m)\mu_2\}$$

where $\alpha_{k-w+1} \equiv l$ and $\alpha_0 \equiv m + 1$, and where A_{mw} satisfies

$$c_{mm}(w, w) = \dfrac{N_1! \, N_2! \, A_{mw}}{(N_1 - w + 1)! \, (N_2 - m + 1)!}$$

(7)

$$= -\sum_{a=1}^{m-1} \sum_{b=1}^{w} c_{ma}(w, b) - \sum_{b=1}^{w-1} c_{mm}(w, b)$$

with $c_{11}(1,1) = A_{11} = 1$; when $l < m$ and/or $k < w$,

(8) $$c_{lm}(k, w) = 0.$$

In the above, we define $\Pi_a^b f(\cdot) \equiv 1$ and $\Sigma_a^b f(\cdot) \equiv 1$ whenever $b < a$.

These results are proved by induction. This is straightforward in principle though necessarily lengthy and tedious in detail. Consequently the details are omitted here but can be found in Billard (1974).

These elements are slightly recursive, in the A_{mw} terms. However, the partitioning employed here makes them less recursive than first appears from the direct use of the recursion theorem. Thus, if we wish to find a particular $A_{m'w'}$, say, we need only consider $w = 1, \cdots, w'$ for each $m = 1, \cdots, m'$ and not all the $w = 1, \cdots, N_1 + 1$ as Severo's theorem suggests.

Since there is a one-to-one correspondence between the points x and the $s(x)$ counting coordinate, the solution to $z_s(t)$ immediately gives the state probability $q(x; t)$. That is,

$$q(x; t) = \sum_{m, w} c_{N_2 - x_2 + 1, m}(N_1 - x_1 + 1, w) \exp(b_{mw} t)$$

where $b_{mw} = b_{mm}(w, w)$. Hence, we may obtain any other quantities of interest such as the distribution of a particular species, its expectation or its probability of extinction.

3. A single species

The results for a single population are in fact embedded within these results for the two-species model. This has the advantage that the corresponding probabilities can easily be extracted although it should be noted that this only makes sense when the actual transition probabilities for that single population do not involve the other population. We illustrate how this is accomplished as follows.

In the particular prey–predator process discribed in this section, the predator species has a death rate proportional to the number of predators present only. Suppose we wish to extract the probabilities $\Pr(X_2 = x_2)$ from the general results of our theorem. We first observe that the ordering of the x points in A was such that for each x_2 we had the sequence $(x_2, N_1), (x_2, N_1 - 1), \cdots, (x_2, 0)$. Further this set of points corresponded to the rows of the sub-block $l = N_2 - x_2 + 1$. We take any particular row k, $k = 1$ say, and suppress the reference to x_1. The resultant solutions are those we would obtain if the X_2 population were operating independently. Note $k = 1$ corresponds to $x_1 = N$. We immediately have that $w = 1$ only. Further, the factors emanating from the term $\delta_0(b_j - b_i)$ in Severo's recursion theorem are expressed by our terms $Q(v)$. When the X_2 population operates independently, the diagonal elements of $\boldsymbol{B}$ become

$$b_{ll}(w, w) = -\mu_2(N_2 - l + 1).$$

Thus, suppressing reference to x_1 is equivalent, in this case, to setting $\mu_1 = 0$ in $Q(v)$. Hence, the non-zero elements become

$$c_{lm}(1, 1) = \frac{(-1)^{l-m}N_2!}{(m-1)!\,(l-m)!\,(N_2 - l + 1)!}.$$

Therefore,

$$\Pr(X_2 = x_2) = \sum_{m=1}^{N_2 - x_2 + 1} c_{N_2 - x_2 + 1, m}(1, 1)\exp\{-\mu_2 t(N_2 - m + 1)\}$$

$$= \frac{N_2!}{x_2!\,(N_2 - x_2)!}\exp(-\mu_2 t x_2)\sum_{r=0}^{N_2 - x_2}\binom{N_2 - x_2}{r}(-\exp(-\mu_2 t))^{N_2 - x_2 - r}$$

$$= \binom{N_2}{x_2}\exp(-\mu_2 t x_2)(1 - e^{-\mu_2 t})^{N_2 - x_2}, \qquad x_2 = 0, \cdots, N_2,$$

which is the familiar result for a simple death process whose death rate is μ_2.

That the results for the one-dimensional process can be obtained so readily highlights an advantage of the partitioning scheme used in conjunction with the Severo method. Whilst we shall not attempt a mathematical formulation here, it can be shown that by generalising the procedure used in this paper, we can handle the case where s species are interacting.

References

BARTLETT, M. S. (1957) On theoretical models for competitive and predatory biological systems. *Biometrika* **44**, 27–42.

BARTLETT, M. S. (1960) *Stochastic Population Models in Ecology and Epidemiology*. Methuen, London.

BARTLETT, M. S., GOWER, J. C. AND LESLIE, P. H. (1960) A comparison of theoretical and empirical results for some stochastic population models. *Biometrika* **47**, 1–11.

BECKER, N. G. (1970) A stochastic model for two interacting populations. *J. Appl. Prob.* **7**, 544–564.

BILLARD, L. (1974) Properties of the stochastic prey–predator model. Technical Report No. 57, Stanford University.

LESLIE, P. H. (1948) Some further notes on the use of matrices in population mathematics. *Biometrika* **35**, 213–245.

LESLIE, P. H. AND GOWER, J. C. (1958) The properties of a stochastic model for two competing species. *Biometrika* **45**, 316–330.

LOTKA, A. J. (1925) *Elements of Physical Biology*. Williams and Wilkins, Baltimore.

MERTZ, D. B. AND DAVIES, R. B. (1968) Cannibalism of the pupal stage by adult flour beetles: An experiment and a stochastic model. *Biometrics* **24**, 247–275.

NEYMAN, J., PARK, T. AND SCOTT, E. L. (1956) Struggle for existence: the *Tribolium* models, biological and statistical aspects. *Proc. 3rd Berkeley Symp. Math. Statist. Prob.* **4**, 41–79.

PARK, T. (1954) Experimental studies of interspecies competition II. Temperature, humidity and competition in two species of *Tribolium*. *Physical Zool.* **27**, 177–238.

PURI, P. S. (1975) A linear birth and death process under the influence of another process. *J. Appl. Prob.* **12**, 1–17.

SEVERO, N. C. (1967) Two theorems on solutions of differential-difference equations and applications to epidemic theory. *J. Appl. Prob.* **4**, 271–280.

SEVERO, N. C. (1969a) A recursion theorem on solving differential-difference equations and applications to some stochastic processes. *J. Appl. Prob.* **6**, 673–681.

SEVERO, N. C. (1969b) Right-shift processes. *Proc. Nat. Acad. Sci.* U.S.A. **64**, 1162–1164.

SEVERO, N. C. (1971) Multidimensional right-shift processes. *Adv. Appl. Prob.* **3**, 200–201.

VOLTERRA, V. (1926) Variazoni e fluttazioni del numero d'individui in specie animali conviventi. *Mem. Acad. Lincei Roma* **2**, 31–113.

VOLTERRA, V. (1931) *Leçons sur la théorie mathématique de la lutte pour la vie.* Gauthier–Villars, Paris.

WEISS, G. H. (1963) Comparison of a deterministic and a stochastic model for interaction between antagonistic species. *Biometrics* **19**, 595–602.