PROPERTIES OF THE STOCHASTIC PREY-PREDATOR MODEL

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L. BILLARD

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Introduction

Questions relating to the coexistence of species have long been of interest to the ecologist. The ecologist wants to know whether two or more species can continue to survive in some environment, or whether one or more species eventually becomes extinct. He is also interested in how the carrying capacity of the environment affects the population sizes of the species. Darwin (1869, p. 80) said "each species, even where it most abounds, is constantly suffering enormous destruction at some period of its life, from enemies or from competitors for the same place and food." The usual outcome is the departure of a species either by actual extinction or by removal to some other environment. For example, the appearance in South America of carnivorous mammals of the Felidae family resulted in the disappearance of carnivorous marsupials. More recently, concern over the destruction of sugar-cane by rats induced Jamaica to introduce mongoose to eliminate the rats.

Lotka (1925) and Volterra (1926, 1931) established mathematical equations for these processes in a deterministic situation. When there are two or more species present, the resultant interaction between species give models which even in the deterministic form are
difficult to solve. So far, models have been defined for competition between species where species compete for the same food supply etc., and prey-predator interaction in which one species constitutes the food supply of the other. This latter is sometimes referred to as host-parasite interaction. Feller (1939) first considered establishing stochastic versions of deterministic models. Unfortunately, they were considered so intractable mathematically that virtually no progress on this important problem has been made. What little work there exists concerning the stochastic model is largely confined to discussion of simulation results using a deterministic model as a starting point. Chiang (1954) provides the appropriate partial differential equation for the moment generating function for two models and the corresponding differential-difference equations. An example in Kendall (1952) is a special case of these processes.

By confining our attention to the prey-predator process, this paper aims to dispel the myth of mathematical intractability. By considering first the model in which no growth occurs, we show how the resulting equations can be transformed into a tractable system of equations. This together with expressions for the state probabilities are found in Section 3. In Section 4, we consider the more general model which permits growth in population sizes. We begin with a brief resume of previous work on these models.
2. **Previous work**

Define \( X_1(t) \) as the number of prey present at time \( t \), and \( X_2(t) \) as the number of predators present at time \( t \). The Lotka-Volterra equations are

\[
\frac{dX_1(t)}{dt} = (\lambda_1 - \mu_1 X_2(t)) \cdot X_1(t) \tag{1}
\]

\[
\frac{dX_2(t)}{dt} = (-\mu_2 + \lambda_2 X_1(t)) \cdot X_2(t) \tag{2}
\]

where the parameters are interpreted as: \( \lambda_1 \) is the rate of increase of the prey species, \( \mu_1 X_2(t) \) is the rate of decrease in the prey species due to predation, \( \mu_2 \) is the rate of decrease of the predator species, and \( \lambda_1 X_1(t) \) is the rate of increase in the predator species due to the presence of the prey species.

From these equations, we obtain

\[
f(X_1, X_2) = -\mu_2 \ln X_1(t) - \lambda_1 \ln X_1(t) + \lambda_2 X_1(t) + \mu_1 X_2(t) = \text{constant} \tag{3}
\]

For cycles near the equilibrium point which from equations (1) and (2) is easily seen to be \( (X_1, X_2) = (\mu_2/\lambda_2, \lambda_1/\mu_1) \), the closed curves given by equation (3) will approximate to the ellipses

\[
\frac{\mu_2 a^2}{2} + \frac{\lambda_1 b^2}{2} = \text{constant}
\]

where \( X_1(t) = X_1(1+a), X_2(t) = X_2(1+b) \).
If $X_1$, say, is small, it is clear that fluctuations introduced by a stochastic element will result eventually in the extinction of the prey species. In this instance, extinction of the prey ultimately leads to the extinction of the predators by starvation. Discussion of simulation studies on this aspect is given by Bartlett (1957, 1960).

After an analysis of data provided by Gause (1934) in which the cultures Paramecium aurelia and Paramecium caudatum feed upon Bacillus pyocyaneus, Leslie (1948) modified the equations (1) and (2). The Lotka-Volterra equations provide no upper limit to the relative rate of increase of the predator species. Leslie suggested that the equation (2) be replaced by

$$\frac{dX_2(t)}{dt} = \left(\mu_2 - \frac{\lambda_2 X_2(t)}{X_1(t)}\right)X_1(t)$$  \hspace{1cm} (4)

Thus, if $X_1(t)$ increases to infinity, the rate of change of $X_2(t)$ approaches $\mu_2 X_2(t)$ which is just the intrinsic rate of increase of the predator species living alone. Likewise, if $X_1(t)$ decreases to zero, $dX_2(t)/dt \to -\infty$ which corresponds to the extinction of the predator species in the absence of its food supply, that is, the prey species.

Other modifications to the basic Lotka-Volterra equations can be made to incorporate various aspects of the populations. For example, the prey species if allowed to increase indefinitely, would approach a saturation point as it must survive in the existing limited environment. This point was first made by Verhulst (1845). Leslie (1948) also considered this concept, replacing equation (1) by
\[
\frac{dX_i(t)}{dt} = \left( \lambda_i - rX_i(t) - \mu_i X_2(t) \right) / X_i(t),
\]

Leslie and Gower (1960) give the discrete time analogues of equations (4) and (5), viz.,

\[
X_1(t+1) = \frac{\lambda_1 X_1(t)}{1 + \alpha_1 X_1(t) + \beta_1 X_2(t)},
\]

\[
X_2(t+1) = \frac{\lambda_2 X_2(t)}{1 + \alpha_2 X_2(t)/X_1(t)},
\]

where \( r_i = \ln \lambda_i, i = 1, 2 \) are the intrinsic rates of increase of the respective species and \( \alpha_1, \alpha_2, \beta \) are positive parameters. Using simulated data, they discuss the behavior of the stochastic behavior of the stochastic discrete-time model corresponding to the equations (6) and (7), in the region of the equilibrium state.

Quite obviously the Lotka-Volterra equations can be modified in many ways to forms suggested by actual data or the investigator's view of reality. However, it can be argued that more general models are already included in equations (1) and (2) if the linear growth rate of a particular individual in a species is viewed as a first approximation in a Taylor expansion about the equilibrium point [Lotka (1925, p. 62)].
3. The Stochastic Model When no Growth Occurs

By no growth, we mean that in the time under consideration new individuals are not added to the species by births or immigration. However, the prey species suffer losses by predation, and deaths can occur to the predator species.

Let $X_1(t)$ and $X_2(t)$ be the size of the prey and predator species at time $t$, respectively and let $\mu_1$, $\mu_2$ be the death parameters. Let $\mathbf{X}(t) = (X_1(t), X_2(t))$ have realization $\mathbf{x} = (x_1, x_2)$ with 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 $e_1 = (1, 0)$ and $e_2 = (0, 1)$. Then, assuming mixing is homogeneous and that two or more transitions occur in the interval $(t, t+h)$ with probability $o(h)$, the transition probabilities are

$$\Pr(\mathbf{x} + e_1 \to \mathbf{x}) = \mu_1(x_1 + 1)x_2 h + o(h)$$

$$\Pr(\mathbf{x} + e_2 \to \mathbf{x}) = \mu_2(x_2 + 1)h + o(h)$$

$$\Pr(\mathbf{x} \to \mathbf{x}) = 1 - x_2(\mu_1 x_1 + \mu_2)h + o(h).$$

Writing

$$q(x; t) = \Pr(\mathbf{X}(t) = x | \mathbf{X}(0) = x_0),$$

$$6$$
the differential-difference equation is

\[
q'(x; t) = -x_2(\mu_1x_1 + \mu_2) q(x; t) + \mu_1(x_1 + 1)x_2 q(x + e_1; t) + \mu_2(x_2 + 1) q(x + e_2; t) \quad \text{for } x \text{ in } A \quad (8)
\]

The corresponding partial differential equation for the moment generating function is

\[
\frac{\partial M}{\partial t} = \mu_1(e^{-\phi_1} - 1) \frac{\partial^2 M}{\partial \phi_1 \partial \phi_2} + \mu_2(e^{-\phi_2} - 1) \frac{\partial M}{\partial \phi_2} \quad (9)
\]

where \( M = M(\phi_1, \phi_2; t) = \delta(\exp(\phi_1x_1(t) + \phi_2x_2(t)) \}. \) It is easier however to work with the differential-difference equations (8).

The prey-predator model formulated here is a two-dimensional pure death process. Severo (1969a, Section 3) has shown how the equations for any multidimensional pure death process can be transformed into a system whose equations can be solved by a recursion theorem given in the same paper (Theorem 1).

To every point \( x \) in \( A \) there is a corresponding \( k = k(x) \).

On applying Severo (1969, equation (4)) to the present problem, we find \( k \) is given by

\[
k = k(x) = (N_1+1)(N_2+1) + x_2 - (N_2+1)x_1. \quad (10)
\]

Similarly, we obtain
\[ k(x + e_i) = k(x) - h_i, \quad i = 1, 2 \]

where

\[ h_1 = 1, \quad h_2 = (N_1 + 1). \]

Hence, writing

\[ z_k(t) \equiv q(x; t) \]

the equations (8) become

\[ z_k'(t) = -x_2(\mu_1 x_1 + \mu_2) z_k(t) + \mu_1(x_1 + 1)x_2 z_{k-1}(t) \]
\[ + \mu_2(x_2+1) z_{k-N_1-1}(t), \quad k = 1, \ldots, (N_1+1)(N_2+1) \quad (11) \]

In matrix form, we have

\[ z'(t) = B z(t) \quad (12) \]

where the matrix of coefficients is clearly lower triangular. Hence application of Severo (1969a, Theorem 1) yields the solution in the form

\[ z(t) = C e(t) \]
where $e(t)$ has components $\exp(b_{i i} t)$ with $b_{i i}$ being the $i$th diagonal element of $B$, and where the elements $C(i, j)$ of $C$ are as provided by the theorem. The $C(i, j)$ are in general functions of $t$, viz.,

$$C(i, j) = C_0(i, j) + t C_1(i, j) + \cdots + t^{i-j} C_{i-j}(i, j).$$

Before deriving the $C(i, j)$ let us make a closer examination of the structure of the matrix $B$. Therefore, let us partition $B$ as

$$B = (B_{\ell m}), \quad \ell, m = 1, \ldots, N + 1$$

where

$$B_{\ell m} = (B_{\ell m}(k, w)), \quad k, w = 1, \ldots, N + 1$$

are $(N_1 + 1) \times (N_1 + 1)$ matrices.

Referring to equation (11), it is immediately clear that

$$B_{\ell \ell}(k, w) = \begin{cases} -(N_2-\ell+1) [\mu_1(N_1-k+1) + \mu_2], & w + k \\ (N_2-\ell+1) [\mu_1(N_1-k+2) + \mu_2], & w = k-1 \\ 0, & \text{otherwise} \end{cases}$$

$$B_{\ell \ell-1}(k, w) = \begin{cases} \mu_2(N_2-\ell+2), & w = k \\ 0, & \text{otherwise} \end{cases}$$

$$B_{\ell m} = 0 \quad m \neq \ell, \ell-1.$$
Similarly, let us partition \( C \) as

\[
C = (C_{\ell m}) , \quad \ell, m = 1, \ldots, N_2 + 1
\]

where

\[
C_{\ell m} = (C_{\ell m}(k,w)) , \quad k, w = 1, \ldots, N_1 + 1 .
\]

We then have the following result for parameter values such that

\[
(\mu_1 x_1 + \mu_2) \neq (\mu_1 x'_1 + \mu_2) \quad \text{for } x_1 \neq x'.
\]

In this case we readily find that \( C(i,j) = C_0(i,j) \), independent of \( t \).

When \( \ell > m, k > w, \)

\[
C_{\ell m}(k,w) = \frac{\mu_1^{k-w} \mu_2^{\ell-m} N_1^i N_2^i A_{mn}}{(N_1-\ell+k+1)! (N_2-\ell+1)!} \prod_{v=1}^{k-w} [V(v)]
\]

where

\[
V(v) = \frac{i_{v+1}}{i_v} \prod_{i_v=m}^{i_{v+1}} \frac{(N_2-i_v+1)/Q(v)}
\]

with

\[
Q(v) = \prod_{j_v=i_v}^{i_{v+1}} [-\mu_1 ((j_v-m) (N_1-v+w-1) + v(N_2-m+1)) - (j_v-m) \mu_2]
\]

where \( i_{k-w+1} \equiv \ell \) and \( i_0 \equiv m+1 \), and where \( A_{mn} \) satisfies
\[ C_{mn}(w, w) = \frac{N_1! N_2! A_{mw}}{(N_1-w+1)! (N_2-m+1)!} \]

\[ = - \sum_{a=1}^{m-1} \sum_{b=1}^{w} C_{ma}(w, b) - \sum_{b=1}^{w-1} C_{mn}(w, b) \quad (14) \]

When \( k < m \) and/or \( k < w \),

\[ C_{km}(k, w) = 0 \quad (15) \]

These results can be proved by induction. Since the four coordinates \((\ell, k)\) and \((m, w)\) uniquely correspond to the two coordinates \(i\) and \(j\), it is sufficient to conduct just a two-way induction procedure, applying at each stage the appropriate part of Severo's Theorem 1. This is straightforward in principle though necessarily lengthy and tedious in detail. (See the Appendix.) The zeros in \( C \) follow more readily. Thus, the case \( \ell < m \) corresponds simply to Severo's \( i < j \). The \( k < m \) case follows by induction using initially the result that the \( \ell < m \) elements are zero.

Since there is a one-to-one correspondence between the points \( x \) and the \( k(x) \) coordinate, finding the solution to \( z_k(t) \) immediately gives us the state probabilities \( q(x; t) \). Hence, by summing over \( x_2 \) (or \( x_1 \)) we obtain the distribution of the number of prey (or predators) remaining at time \( t \). Clearly, any \( x_1 \) corresponds to \( k = (N_1-x_1+1) \) and \( x_2 \) to \( \ell = N_2-x_2+1 \). Thus,
\[ q(x; t) = \sum_{mw} C_{N_2^{-x_2}+1, m, N_1^{-x_1}+1, w} \exp(b_{mw} t) \] (16)

where \( b_{mw} \equiv B_{mm}(w, w) \)

\[ \Pr(X_1(t) = x_1) = \sum_{\ell} \sum_{mw} C_{\ell m}(N_1^{-x_1}+1, w) \exp(b_{mw} t), \] (17)

\[ \Pr(X_2(t) = x_2) = \sum_{k} \sum_{mw} C_{m, N_2^{-x_2}+1, k, w} \exp(b_{mw} t). \] (18)

Examining these probabilities their combinatorial nature is immediately apparent [compare the normality assumption used in the simulation studies by Leslie and Gower (1960)]. It is also obvious that the factorial moments can be derived directly by noting the \((N_1^{-k+1})!\) and \((N_2^{-\ell+1})!\) components in the denominator of the expression (13). Consequently, simply by omitting leading terms in these factorials, the successive factorial moments can be determined. This is computationally appealing lending greater importance to the usefulness of the original partitioning of the \( B \) matrix. For example,

\[ s(X_1(t)) = \sum_{(\ell, k), (m, w)} \frac{k-w}{(N_1^{-k})!} \frac{\ell-m}{(N_2^{-\ell+1})!} \frac{A_{mw}}{Q(O)} \prod_{v=1}^{k-w} \{V(v)\} \] (19)
4. The Stochastic Model when Growth Occurs

Let us now consider the prey-predator model in which growth of each species can occur. Since the transformation technique itself is independent of the actual form taken by the rate of increase for each species, we shall consider the stochastic analogue of the Lotka-Volterra equations (1) and (2). The corresponding stochastic formulation for other forms such as equations (4) and (5) can be treated analogously and are equally tractable.

Let us denote the number of prey present at time \( t \) by \( X_{11}(t) \) and the number of predators present at time \( t \) by \( X_{21}(t) \). [Clearly, \( X_{11}(t) \equiv X_i(t), i = 1, 2, \) of Section 2.3.] Let \( X_{10}(t) \) be the number of losses in the prey species due to predation, and let \( X_{20}(t) \) be the number of deaths in the predator species up to time \( t \). We introduce a third category which may be interpreted as a source from which births to a species are drawn. If we let \( X_{12}(t) \) be the number remaining in this source at time \( t \) for the prey species, then 

\[ \{X_{12}(0) - X_{12}(t)\} \]

is the number of additions from births to the prey species up to time \( t \). Similarly, \( X_{22}(t) \) is the number remaining in this source for the predator species. The birth and death parameters \( \lambda_i, \mu_i, i = 1, 2 \) are as given in Section 2.

Let \( X = (X_1, X_2) \) where \( X_i = (X_{i2}(t), X_{i1}(t), X_{i0}(t)), i = 1, 2, \) have realization \( \bar{x} = (x_1, x_2) \). The vector \( \bar{x} \) takes values on the space

\[
R = \{0 \leq x_{ij} \leq N_i \text{ with } \sum_{j=0}^{2} x_{ij} = N_i, i = 1, 2, j = 0, 1, 2\} \tag{20}
\]
and where \( N_i = \sum_{j=0}^{2} X_{ij}(0) \) is a finite integer. Define the six-dimensional vector \( \mathbf{e}_{ij}, i = 1, 2 \) and \( j = 0, 1, 2 \) with elements \( \delta_{iu} \delta_{vj}, u = 1, 2 \) and \( v = 0, 1, 2 \). For example, \( \mathbf{e}_{12} = (1, 0, 0; 0, 0, 0) \).

Assuming the populations are mixing homogeneously and that the probability of two or more transitions in the interval \((t, t+h)\) is \( o(h) \), the transition probabilities are

\[
\Pr(\mathbf{x} + \mathbf{e}_{12} - \mathbf{e}_{11} \rightarrow \mathbf{x}) = \lambda_1(x_{11}^{-1})h + o(h)
\]

\[
\Pr(\mathbf{x} + \mathbf{e}_{11} - \mathbf{e}_{10} \rightarrow \mathbf{x}) = \mu_1(x_{11}+1)\mathbf{x}_{11}h + o(h)
\]

\[
\Pr(\mathbf{x} + \mathbf{e}_{22} - \mathbf{e}_{21} \rightarrow \mathbf{x}) = \lambda_2(x_{21}^{-1})\mathbf{x}_{11}h + o(h)
\]

\[
\Pr(\mathbf{x} + \mathbf{e}_{21} - \mathbf{e}_{20} \rightarrow \mathbf{x}) = \mu_2(x_{21}+1)h + o(h)
\]

\[
\Pr(\mathbf{x} \rightarrow \mathbf{x}) = 1 - [x_{11}(\lambda_1 + \mu_1\mathbf{x}_{21}) + x_{21}(\lambda_2\mathbf{x}_{11} + \mu_2)]h + o(h)
\]

Writing

\[
p(x; t) = Pr[X(t) = x | X(0) = x_0]
\]

the differential-difference equations are

\[
p'(x; t) = -[x_{11}(\lambda_1 + \mu_1\mathbf{x}_{21}) + x_{21}(\lambda_2\mathbf{x}_{11} + \mu_2)]p(x; t)
\]

\[
+ \lambda_1(x_{11}^{-1}) p(\mathbf{x} + \mathbf{e}_{12} - \mathbf{e}_{11}; t)
\]

\[
+ \mu_1(x_{11}+1)\mathbf{x}_{21} p(\mathbf{x} + \mathbf{e}_{11} - \mathbf{e}_{10}; t)
\]

\[
+ \lambda_2(x_{21}^{-1})\mathbf{x}_{11} p(\mathbf{x} + \mathbf{e}_{22} - \mathbf{e}_{21}; t)
\]

\[
+ \mu_2(x_{21}+1) p(\mathbf{x} + \mathbf{e}_{21} - \mathbf{e}_{20}; t)
\] for \( x \) in \( R \).

(21)
If we define the moment generating function of \( X_{11}(t) \) and \( X_{21}(t) \) as

\[
M = M(\theta_1, \theta_2; t) = \exp(\theta_1 X_{11}(t) + \theta_2 X_{21}(t))
\]

we can readily verify that the partial differential equation corresponding to (21) is

\[
\frac{\partial M}{\partial t} = \lambda_1(e^{\theta_1} - 1) \frac{\partial M}{\partial \theta_1} + \mu_2(e^{-\theta_2} - 1) \frac{\partial M}{\partial \theta_2}
\]

\[
+ [\mu_1(e^{-\theta_1} - 1) + \lambda_2(e^{\theta_2} - 1)] \frac{\partial^2 M}{\partial \theta_1 \partial \theta_2}.
\]  \((22)\)

However, as in the previous section, we shall work with the differential-difference equations rather than this partial differential equation.

In order to find solutions to the equations (21), we first recognize the prey-predator process modelled here as nothing other than a multidimensional right-shift process described by Severo (1971). We can transform the system of equations (21) into a system whose matrix of coefficients is triangular, by combining the arguments of Severo (1969a, Section 3; and 1969b).

Accordingly, to every \( x \) point in \( \mathbb{R} \) there corresponds a coordinate which we can easily show is given by

\[
k(x) = \binom{N_1+2}{2} \binom{N_2+2}{2}^2 \left[ x_{21} - x_{22}^2/2 + x_{22}(2N_2+3)/2 \right]
\]

\[
- \binom{N_2+2}{2} \left[ x_{11} - x_{12}^2/2 + x_{12}(2N_1+3)/2 \right] \quad . \]  \((23)\)
The $x + e_{ij} - e_{i,j-1}$ points in $\mathbb{R}$ are transformed to

$$k(x + e_{ij} - e_{i,j-1}) = k(x) - h_{ij}, \quad i = 1, 2, \ j = 1, 2$$

where we readily verify that the $h_{ij}$ are given by

$$h_{21} = 1, \quad h_{22} = N_2 - x_{22},$$

$$h_{11} = \binom{N_2 + 2}{2}, \quad h_{12} = \binom{N_2 + 2}{2}(N_1 - x_{12})$$

Writing

$$y_k(t) = p(x; t)$$

the equations (21) become under the transformation (23) and (24),

$$y'_k(t) = \left[ x_{11}(\lambda_1 + \mu_1 x_{21}) + x_{21}(\lambda_2 x_{11} + \mu_2) \right] y_k(t)$$

$$+ \lambda_1(x_{11} - 1) y_{k-h_{12}}(t) + \mu_1(x_{11} + 1)x_{21} y_{k-h_{11}}(t)$$

$$+ \lambda_2(x_{21} - 1)x_{11} y_{k-h_{22}}(t) + \mu_2(x_{21} + 1) y_{k-h_{21}}(t),$$

for $k = 1, \ldots, \binom{N_1 + 2}{2}\binom{N_2 + 2}{2}$

In matrix notation,

$$y'(t) = F y(t).$$

(26)
The matrix of coefficients $F$ is obviously lower triangular, and therefore Severo (1969a, Theorem 1) is applicable to give a solution in the form

$$y(t) = D e(t)$$  \hspace{1cm} (27)$$

where, as before, the $e(t)$ has components $\exp(f_{ii} t)$ where $f_{ii}$ is the $i$th diagonal element of $F$, and the elements $d(i,j)$ of $D$ are found from Severo's theorem.

The form taken by the elements of $D$ is necessarily more complicated algebraically than we saw for the elements of $C$ when no growth occurred. However, computationally the recursion theorem entails the same magnitude of effort in the two cases. More importantly however, we should observe that $F$ is still extremely sparse having at most five non-zero elements in any one row. Therefore, the amount of work involved is considerably less than at first appears. Finally, there will be many "groups" of zero elements in $D$ just as we previously saw existed in $C$.

Again since $x$ point corresponds uniquely to one $k$ coordinate, solution of $y_k(t)$ immediately gives the corresponding $p(x; t)$. Hence, the distribution of any $X_{ij}(t)$, $i = 1, 2$, $j = 0, 1, 2$ can be found. In particular, we have the distribution of the number of prey and/or predators present at time $t$. It is reasonable to conjecture that the factorial moments for this process will also fall out neatly, at least from a computational viewpoint, just as they did when no growth occurred.
For illustrative purposes, we give the $d(i,j)$ values for the case in which $X(0) = (1, 1, 0; 1, 1, 0)$. Thus, $N_1 = N_2 = 2$. Therefore, we obtain the elements of $D$ as:

\[
\begin{align*}
    d(8,8) &= 1 \\
    d(9,8) &= \mu_2/\alpha_{110} = -\alpha_{001} d(12,8)/2\mu_2 = \mu_2 d(14,8)/\mu_1 = d(15,8) \eta_{12}/\mu_1 \\
    d(10,8) &= \lambda_2/\alpha_{001} = -\lambda_2 d(11,8)/2\mu_2 = \eta_{10} d(16,8)/2\mu_1 \\
    d(17,8) &= \eta_{12} d(18,8)/\mu_2 = -2\mu_1 \mu_2 (\eta_{10}-2\lambda_2)/\alpha_{110} \alpha_{001} \eta_{10} \\
    d(20,8) &= \lambda_1/f_{111}; d(21,8) = \lambda_1 \mu_2 f_{200}/\eta_{12} \alpha_{101} f_{111} \\
    d(22,8) &= \lambda_1 \lambda_2 (f_{231} + \mu_2)/f_{231} \alpha_{001} f_{111}; \\
    d(23,8) &= 2\mu_2 \lambda_1 (\lambda_2 + f_{110} f_{231})/\alpha_{010} \alpha_{001} f_{231} f_{111} \\
    d(24,8) &= 2\lambda_1 \mu_2 (\lambda_1 \alpha_{050} - \alpha_{010} f_{110} f_{231})/\eta_{12} \alpha_{001} \alpha_{110} \alpha_{010} f_{111} f_{231} \\
    d(26,8) &= -2\mu_1/f_{111} = \eta_{12} d(27,8)/\mu_2 \\
    d(28,8) &= -4\mu_1 \lambda_2 (\eta_{12} + 2\mu)/f_{211} f_{111} f_{231} \alpha_{001} \\
    d(29,8) &= -4\mu_1 \mu_2 [(\lambda_1 + \lambda_2) f_{231} \alpha_{010} + \lambda_1 \lambda_2 \mu_2 (3\alpha_{010} + \mu_2)] \\
    &\quad \div (\lambda_1+\lambda_2) f_{111} f_{231} \alpha_{001} \alpha_{010} f_{211} = d_1 \\
    d(30,8) &= \mu_2 d_1/\eta_{12} \\
    d(32,8) &= -2\mu_2^2/\alpha_{110} f_{111} = \eta_{12} d(33,8)/\mu_2 \\
    d(34,8) &= -8\mu_1^2 \lambda_2 (\eta_{12} - 2\gamma_1)/\eta_{10} f_{211} f_{111} f_{231} \alpha_{001} = d_2 \\
    d(35,8) &= (\mu_1 d_1 + 2\mu_2 d_2)/\alpha_{110} = \eta_{12} d(36,8)/\mu_2; d(i,8) = 0, i = 13, 19, 25, 31
\end{align*}
\]
\[
\begin{align*}
d(9, 9) &= -\mu_2 / \alpha_{110} = -d(21, 9); \quad d(i, 9) = 0, \; i \neq 9, 21 \\
d(10, 10) &= -\lambda_2 / \alpha_{001} = \gamma_1 d(11, 10) / 2\mu_2 = \gamma_1^2 d(12, 10) / \mu_2^2 = f_{120} d(16, 10) / 2\mu_1 \\
d(17, 10) &= -2\mu_1 \mu_2 \lambda_2 f_{340} / f_{220} \gamma_1 f_{120} \alpha_{001} = f_{320} d(18, 10) / \mu_2 \\
d(22, 10) &= -\lambda_1 \lambda_2 / \eta_{21} \alpha_{001} = f_{200} \gamma_1 d(23, 10) / 2\mu_2 = -\lambda_1 d(28, 10) / 4\mu_1 \\
d(24, 10) &= -\lambda_1 \lambda_2 \mu_2^2 (f_{220} f_{300} + 2\mu_1 \gamma_1) / f_{320} \gamma_1 f_{200} \eta_{21} \alpha_{001} \\
d(29, 10) &= -4\mu_1 \mu_2 \lambda_2 (f_{200} \eta_{11} - \lambda_1 \mu_1) \alpha_{001} f_{200} \gamma_1 \eta_{11} \eta_{21} = f_{320} d(30, 10) / \mu_2 \\
d(34, 10) &= 8\mu_1 \lambda_2 / \alpha_{001} f_{120} \eta_{21} \\
d(35, 10) &= 4\mu_1 \mu_2 \lambda_2 [\mu_1 f_{120} - \eta_{11} f_{200} (4\gamma_1 + f_{120})] / \alpha_{001} f_{220} f_{120} \eta_{21} \eta_{11} f_{200} \gamma_1 \\
&= f_{320} d(36, 10) / \mu_2 \\
d(11, 11) &= -2\mu_2 / \gamma_1 = \gamma_1 d(12, 11) / \mu_2 \\
d(17, 11) &= 2\mu_1 \mu_2 / \gamma_1 (\lambda_1 + \mu_1) = \eta_{11} d(18, 11) / \mu_2 = -f_{110} d(35, 11) / 2\mu_1 \\
&= -f_{110} \eta_{11} d(36, 11) / 2\mu_1 \mu_2 \\
d(23, 11) &= 2\mu_2 \lambda_1 / \gamma_1 f_{110} = \gamma_1 \eta_{11} d(24, 11) / \mu_2 f_{200} = \lambda_1 d(29, 11) / 2\mu_1 \\
&= \eta_{11} \lambda_1 d(30, 11) / 2\mu_1 \mu_2 \\
d(12, 12) &= -\lambda_2 \mu_2^2 / \gamma_1^2 \alpha_{101} \\
d(14, 14) &= -\mu_1 / \alpha_{110} = -d(15, 14) \\
d(15, 15) &= -\mu_1 / \eta_{12} \\
2d(16, 16) &= 4\mu_1 \lambda_2 / \eta_{10} f_{120} = -d(17, 16) = 2d(18, 16) \\
d(17, 17) &= -d(18, 17) = -(\tau_8 + \tau_{10} + \tau_{11} + \tau_{16}), \quad \tau_1 = d(17, 1) \\
d(18, 18) &= -(\tau_8 + \tau_{10} + \tau_{11} + \tau_{16} + \tau_{17}), \quad \tau_1 = d(18, 1)
\end{align*}
\]
\[ d(20, 20) = -\lambda_1^2 f_{111} = \xi_3 \; d(21, 20)/\mu_2 = \xi_3 \; d(22, 20)/2\lambda_2 \]
\[ = \xi_3 \; d(23, 20)/2\mu_2 \; \quad d(24, 20) = 2\lambda_1^2 f_{111} \xi_3 \; \xi_3 \]
\[ d(26, 20) = -4\lambda_1^2 f_{111} \xi_3 \; d(27, 20)/\mu_2 \]
\[ d(28, 20) = -4\mu_1 \lambda_1 \xi_3 \; d(29, 20) = \xi_3 \; d(30, 20)/\mu_2 \]
\[ d(32, 20) = -4\mu_1 \lambda_1 \xi_3 \; d(33, 20)/\mu_2 \]
\[ d(35, 20) = (\mu_1 d_4 + 4\mu_1 \mu_2 d_3 + d_4) \xi_3 \; d(36, 20)/\mu_2 \]
\[ d(21, 21) = -\mu_1 \xi_3 \; d(22, 22) = \xi_3 \; d(23, 22)/\mu_2 \]
\[ = \xi_3 \; d(24, 22)/\mu_2 \]
\[ d(22, 22) = \lambda_1 \lambda_2 (2\xi_3 \xi_2 - \lambda_2) \eta_2 \xi_3 \; d(23, 22)/2\mu_2 \]
\[ = \xi_3 \; d(24, 22)/\mu_2 \]
\[ d(23, 23) = \xi_3 \; d(24, 23)/\mu_2 \]
\[ d(24, 24) = -d(28, 22)/2 = -d(29, 22)/4\mu_2 \]
\[ = -d(30, 22)/2\mu_2 \]
\[ d(26, 26) = -4\mu_1 \xi_3 \; d(27, 26)/\mu_2 = -d(28, 26)/2\mu_2 = -\lambda_2 \xi_3 \; d(30, 26)/2\mu_2 \]
\[ = -\lambda_2 \xi_3 \; d(31, 26)/2\mu_2 \]
\[ d(32, 32) = -4\mu_1 \xi_3 \; d(33, 26)/\mu_2 = -d(34, 26)/4\xi_3 \xi_2 \]
\[ d(35, 25) = -16\mu_1 \mu_2 (2\xi_3 \xi_2 - \lambda_2) \xi_3 \; d(36, 26)/\mu_2 \]
\[ = -16\mu_1 \xi_3 \xi_2 \xi_2 \]

\[ \tau_1 = d(23, 1) \]
\[ \tau_1 = d(24, 1) \]
\[ \tau_1 = d(26, 26) \]
\[ \tau_1 = d(32, 26) \]
\[ \tau_1 = d(35, 26) \]
\[ d(27,27) = 2\mu_1\mu_2[(\eta_{12}^{-1} + 2\xi_{24}^{-1} \xi_{34}^{-1})/\xi_{111} + 2/\xi_{34}^2 \alpha_{101}^{\prime}] \]
\[ d(28,28) = \tau_1^2 d(29,28)/2\mu_2 = \tau_1^2 d(30,28)/\mu_2 = -d(34,28) = \tau_1^2 d(35,28)/2\mu_2 = -d(34,28), \quad \tau_1 = d(28,1) \]
\[ d(29,29) = \tau_1^2 d(30,29)/\mu_2 = -d(35,29) = -\tau_1^2 d(36,29)/\mu_2 = -d(35,29), \quad \tau_1 = d(29,1) \]
\[ d(30,30) = -d(31,30) = -(\tau_1 + \tau_{10} + \tau_{11} + \tau_{20} + \tau_{22} + \tau_{23} + \tau_{26} + \tau_{28} + \tau_{29}), \quad \tau_1 = d(30,1) \]
\[ d(32,32) = -\lambda_1^2 \mu_1^2/\alpha_{10} \xi_{24}^2 = -d(33,32) \]
\[ d(33,33) = \mu_1^2 \xi_{24}^2 \xi_{111}^2 \alpha_{10}^{-1}(\mu_2 \eta_{12}^{-1}(2\mu_2 \xi_{24}^{-1} - \lambda_1 f_{200}) - \lambda_1 \xi_{34}^{-1}[\mu_2 f_{112} + \xi_{24}^2(2\lambda_1 + \xi_{34}^{-1})]) \]
\[ d(34,34) = -d(35,34)/2 = d(36,34) = -(\tau_8 + \tau_{10} + \tau_{20} + \tau_{22} + \tau_{26} + \tau_{28}), \quad \tau_1 = d(34,1) \]
\[ d(35,35) = -d(36,35) = -(\tau_8 + \tau_{10} + \tau_{11} + \tau_{20} + \tau_{22} + \tau_{23} + \tau_{26} + \tau_{28} + \tau_{29}), \quad \tau_1 = d(35,1) \]
\[ d(36,36) = -(\tau_8 + \tau_{10} + \tau_{11} + \tau_{20} + \tau_{22} + \tau_{23} + \tau_{26} + \tau_{29} + \tau_{33}), \quad \tau_1 = d(36,1) \]

where

\[ \alpha_{ijk} = -j\lambda_1 + (-1)^i j^{-1} j\mu_1 - \lambda_2 + (-1)^i k\mu_2 \]
\[ f_{ijk} = -\lambda_1 + (-1)^j j^{-1} j\mu_1 + (-1)^i j^{-1} k\lambda_2 + (-1)^j j^{-1} (i-1)\mu_2 \]
\[ \eta_{ij} = -\lambda_1 + (-1)^i i\mu_1 + (1-j)\lambda_2 + (1-2)\mu_2 \]
\[ \xi_{ij} = \mu_1 - 2\lambda_2 + (2-1)\mu_2 \]
\[ \gamma_i = -i\mu_1 - \mu_2. \]
Hence, we can find the probabilities. For example,

\[
\begin{align*}
\Pr[\text{no prey left but predator population unchanged}] &= \Pr(\mathbf{X} = (0, 0, 2; 1, 1, 0)) \ y_{32}(t) \\
&= 2\mu_1^2 e^{t\eta_{12}/\alpha_{110}} f_{111} - 4\mu_1^2 t^2 I_{21}(\lambda_1 f_{111} e^{t\xi_{34}} \\
&\quad + 2e^{t\alpha_{101}} + \lambda_1 \alpha_{101} e^{-t\mu_2}) .
\end{align*}
\]
Appendix

Proof of Expression for $C_{\ell m}(k,w)$ when no Growth Occurs

We shall freely use the notation of Severo (1969a, Theorem 1) in the sense he defined it. Let us prove the following lemma.

**Lemma.** For parameter values such that the elements of $C$ are independent of $t$,

$$C_{\ell m}(k,w) = \frac{\gamma}{\delta}$$

where

$$\gamma = \mu_2(N_2 - \ell + 2) C_{\ell-1,m}(k,w) + \mu_1(N_1 - k + 2)(N_2 - \ell + 1) C_{\ell m}(k-1,m)$$

and

$$\delta = -\mu_1[(\ell-m)(N_1 - k + 1) + (k-w)(N_2 - m + 1)] - (\ell-m)\mu_2$$

for $k = 2, \ldots, n_1 + 1$ and $\ell \geq m$. When $k = 1$, the last term in $\gamma$ is omitted.

**Proof.** This corresponds to Severo's $i > j$. Therefore,

$$C(i,j) = b(i, i-1) C(i-1, j) h(j, i) .$$

The $((\ell-2)(N_1+1) + k)$th element of $b(i, i-1)$ is $\mu_2(N_2 - \ell + 2)$, and the last element is $\mu_1(N_1 - k + 2)(N_2 - \ell + 1)$ with all other elements zero.
Since the \( C \) elements are independent of \( \tau \), \( C_{\rho}(i,j) = 0 \) for 
\( \rho = 1, \ldots, i-j \). Hence all elements in columns other than the first 
column of \( C(i-1, j) \) are zero. Therefore, we only need to find 
\( \delta_0(b_{j-b_i}) \) in \( h(j,i) \). This we readily see equals our \( \delta \). Applying 
Severo's theorem the lemma follows.

It is now clear that even if \( b_{j-b_i} = 0 \) so that \( \delta_0(b_{j-b_i}) = \tau \), 
the corresponding \( C_{\ell m}(k,w) \) is a function of \( \tau \) only if \( \gamma \neq 0 \). Thus, 
we can write \( C_{\ell m}(k,w) \) is dependent on \( \tau \) if

\[
\gamma \neq 0 \text{ whenever } \delta = 0
\]

and \( C_{\ell m}(k,w) \) is independent of \( \tau \) otherwise.

Proof of \( C_{\ell m}(k,w) \) Expressions.

(a) Let us first consider the zeros. The case \( \ell < m \) corresponds to 
Severo's \( i < j \); so that the result follows immediately.

We prove the case \( k < w \) by induction on \((\ell, k)\) for any 
\((m, w)\) column. First take \( C_{m+1,m}(1,2) \). By the lemma

\[
C_{m+1,m}(1,2) = \mu_2(N_1^{-m+2}) C_{mm}(1,2) / \delta
\]

But \( C_{m,m}(1,2) = C((m-1)(N_1+1) + 1, (m-1)(N_1+1) + 2) = 0 \). Therefore, 
\( C_{m+1,m}(1,2) = 0 \).

Assume the result is true for \( \ell = m+1, \ldots, \ell-1 \) with 
\( k_0 = 1, \ldots, k \) and \( \ell_0 = \ell \) with \( k_0 = 1, \ldots, k-1 \). We want
to prove the result for $\ell_0 = \ell$ with $k_0 = k$. By the lemma,

\[ C_{\ell m}(k, w) = \delta^{-1} \{ \mu_2 (N_2 - \ell + 2) C_{\ell - 1 m}(k, w) \]

\[ + \mu_1 (N_1 - k + 2) (N_2 - \ell + 1) C_{\ell m}(k - 1, w) \} \]

But $C_{\ell - 1, m}(k, w) = 0$ and $C_{\ell m}(k - 1, w) = 0$ were assumed true. Therefore, $C_{\ell m}(k, w) = 0$ for all $k < w$.

(b) Let us now consider the other elements of $C$, making first an induction proof on $(\ell, k)$ for $(m, w) = (1, 1)$. First take $(\ell, k) = (1, 1)$. By Severo's theorem

\[ C_{11}(1, 1) = C(1, 1) = a_1 = 1 \]

It is easily seen that $C_{\ell m}(k, w) = 1$ for $\ell = k = m = w = 1$.

Assume the result is true for $\ell_0 = 1, \ldots, \ell - 1$ with

$k_0 = 1, \ldots, k$ and $\ell_0 = \ell$ with $k_0 = 1, \ldots, k - 1$. We want to prove it is true for $\ell_0 = \ell$ with $k_0 = k$. By the lemma,

\[ C_{\ell 1}(k, 1) = \delta^{-1} \frac{\mu_2 (N_2 - \ell + 2) \mu_1^{k-1} \mu_2^{\ell-2} N_1! N_2! A_{11}}{(N_1 - k + 1)! (N_2 - \ell + 2)!} P(\ell, 1; k, 1) \]

\[ + \frac{\mu_1 (N_1 - k + 2) (N_2 - \ell + 1) \mu_1^{k-2} \mu_2^{\ell-1} A_{11}}{(N_1 - k + 2)! (N_2 - \ell + 1)!} P(\ell, 1; k - 1, 1) \]

where
\[
P(\ell, m; k, w) = \prod_{v=1}^{k-w} V(v) Q_v^{-1}(0)
\]

That is,
\[
C_{\ell 1}(k, l) = \frac{\mu_1^{k-l} \mu_2^{l-1} N_1! N_2! A_{11}}{(N_1-k+1)! (N_2-l+1)!} \left( \frac{P(\ell-1, l; k, l)}{\delta} + \frac{(N_2-l+1)P(\ell, l; k-1, l)}{\delta} \right)
\]

But
\[
\delta^{-1} P(\ell-1, l; k, l) = P(\ell, l; k, l) - \alpha
\]

where \(\alpha\) is the term corresponding to \(i_k = \ell\) in \(P(\ell, l; k, l)\).

It is readily seen that
\[
\delta^{-1}(N_2-\ell+1) P(\ell, l; k-1, l) = \alpha.
\]

Hence,
\[
C_{\ell 1}(k, l) = \frac{\mu_1^{k-1} \mu_2^{l-1} N_1! N_2! A_{11}}{(N_1-k+1)! (N_2-l+1)!} P(\ell, l; k, l).
\]

Thus, the result is true for all \(C_{\ell 1}(k, l)\).

(c) We now make an induction proof on \((m, w)\). The case \((m, w) = (1, 1)\) has been proved in (b). Assume the result is true for \(m_0 = 1, \ldots, m-1\) with \(w_0 = 1, \ldots, w\) and \(m_0 = m\) with \(w_0 = 1, \ldots, w-1\). We want to prove the result for \(m_0 = m\) with \(w_0 = w\). This requires first proving
Thus, we need to consider \( A_{\text{mw}} \). This follows by applying Severo's theorem for \( i = j \). Since the results are assumed true for \( m_0 < m \) and \( w_0 < w \), the expression for \( A_{\text{mw}} \) is true. Hence when \((\ell, k) = (m, w)\), the result is true.

Remaining with the \((m, w)\) column, we assume the result is true for \( \ell_0 = 1, \ldots, \ell-1 \) with \( k_0 = 1, \ldots, k \) and \( \ell_0 = \ell \) with \( k_0 = 1, \ldots, k-1 \). We want to prove the result for \( \ell_0 = \ell \) with \( k_0 = k \). By the lemma,

\[
C_{\ell m}(k, w) = 8^{-1} \frac{\mu_2(N_2 - \ell + 2) \mu_1^{k-w} \mu_2^{\ell-1-m} N_1 \cdot N_2 \cdot A_{\text{mw}}}{(N_1 - k + 1)! (N_2 - \ell + 2)!} \times P(\ell - 1, k; m, w)
+ \frac{\mu_2(N_1 - k + 2)(N_2 - \ell + 1) \mu_1^{k-1-w} \mu_2^{\ell-m} N_1 \cdot N_2 \cdot A_{\text{mw}}}{(N_1 - k + 2)! (N_2 - \ell + 1)!}
\times P(\ell, k-1; m, w)
\]

But

\[
8^{-1} P(\ell - 1, k; m, w) = P(\ell, k; m, w) - \beta
\]

where \( \beta \) is the term corresponding to \( i_{k-w} = \ell \) in \( P(\ell, k, m, w) \).

However, we see
\[ 8^{-1}(N_2-\ell+1) \ P(\ell, k-1; m, w) = \beta \ . \]

Hence,

\[ C_{\ell m}(k, w) = \frac{\mu_1^{k-w} \mu_2^\ell \ N_1! N_2! A_{n w}}{(N_1-k+1)! (N_2-\ell+1)!} \ P(\ell, m; k, w) \ . \]

Thus, the result is true for all \((\ell, m; k, w)\).
References


