

An Age-Stage Population Model

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Abstract

A discrete age-stage population model is proposed. The model is found to behave in many ways like the Leslie model. In particular, the characteristic equation of the age-stage model is similar to that of the Leslie model. Several results already proven for the Leslie model immediately follow: A sufficient condition on non-zero birth rates is found for a stable population distribution. This distribution decreases exponentially with age. Harvesting policies are also investigated, but few results are found.

1 Introduction

A simple, discrete time model which predicts the age distribution of a population is the Leslie model. In matrix form, this model is given by

$$\mathbf{x}(t+1) = \mathbf{L}\mathbf{x}(t)$$

where $\mathbf{x}(t)$ is an n -vector giving the number of individuals in each age class at time t . \mathbf{L} is a square matrix of order n . The first row of \mathbf{L} contains the birth rates for each age class, and the first subdiagonal contains the $n - 1$ survival rates for each age class. \mathbf{L} is called the Leslie matrix.

In practice, it is hard to determine the age of many organisms (fish, for example). It is much easier to classify organisms by some other characteristic, such as their size. A natural extension of the Leslie model, then, is to let $\mathbf{x}(t)$ represent the number of individuals in each *size* class at time t . In this model, an organism may grow from one size class to the next in one time period or may remain in the same size class. However, because an organism may stay in the same size class for an infinite amount of time, this model exhibits unusual behavior in certain contrived situations.

2 Models

Consider a model in which the population is divided into age classes *and* size classes. All new borns enter the world at age 1, size 1. In one time period,

an organism advances to the next age class and may or may not advance to the next size class. Birth rates for each age-size combination are specified. A graphic representation of this model (with K age classes and $L < K$ size classes) is shown below.

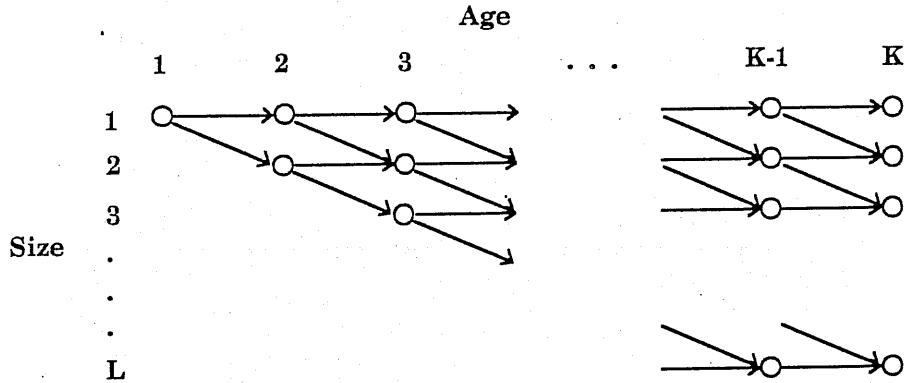


Figure 1: Representation of the *age-size* model

Note that it is possible to prune this graph. For instance, for a given population, it may be reasonable to assume that if an organism has not grown out of size class 1 by age 5, the organism is dead. By pruning edges, it is possible to restrict certain age-size combinations.

Let us call this the *age-size* model. It turns out that many properties of the *age-size* model hold in more general situations. Therefore, I will consider a generalization of this model (which I call the *age-stage* model). The main theorems of this paper will be proved for the *age-stage* model. They are hence proved for the *age-size* model.

Suppose we divide a population into K age classes and L stage classes. A stage class can represent any number of things. For example, a stage can represent a size classification (as above). A stage class can represent a particular body color of an organism, or a particular combination of size, body color, *and* wing span, for example. Let the ordered pair (i, j) represent being in age class i and stage class j . Let $x_{ij}(t)$ = the number of organisms in state (i, j) at time t . Suppose that in one time period an organism advances to the next age class (or dies) and can enter *any* of the L stage classes. Let q_{ijk} = the probability an organism in state (i, j) enters state $(i + 1, k)$. Suppose also that *all* organisms are born into state $(1, 1)$. Let b_{ij} = the birth rate of an organism in state (i, j) . As before, we can represent this model graphically.

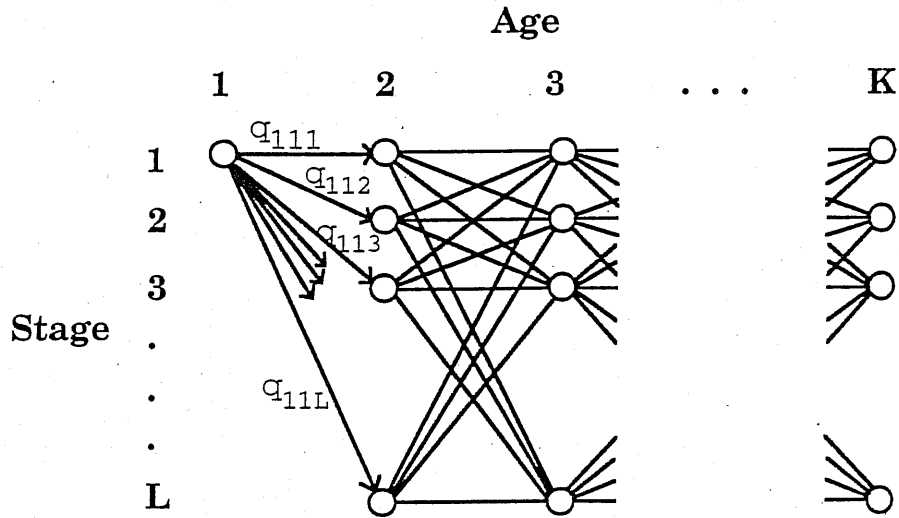


Figure 2: Representation of the *age-stage* model

Let $x(t)$ be a KL -vector in which $x_{ij}(t)$ is at row $(i-1)L + j$. Let

$$M = \begin{bmatrix} b_{11} & \cdots & b_{1L} & \cdots & b_{K-1,1} & \cdots & b_{K-1,L} & b_{K1} & \cdots & b_{KL} \\ 0 & \cdots & 0 & \cdots & 0 & \cdots & 0 & 0 & \cdots & 0 \\ \vdots & & \vdots & & \vdots & & \vdots & \vdots & & \vdots \\ 0 & \cdots & 0 & \cdots & 0 & \cdots & 0 & 0 & \cdots & 0 \\ q_{111} & \cdots & q_{1L1} & \cdots & 0 & \cdots & 0 & 0 & \cdots & 0 \\ \vdots & & \vdots & & \vdots & & \vdots & \vdots & & \vdots \\ q_{11L} & \cdots & q_{1LL} & \cdots & 0 & \cdots & 0 & 0 & \cdots & 0 \\ & & & \ddots & & & & & & \\ 0 & \cdots & 0 & \cdots & q_{K-1,1,1} & \cdots & q_{K-1,L,1} & 0 & \cdots & 0 \\ \vdots & & \vdots & & \vdots & & \vdots & \vdots & & \vdots \\ 0 & \cdots & 0 & \cdots & q_{K-1,1,L} & \cdots & q_{K-1,L,L} & 0 & \cdots & 0 \end{bmatrix}$$

Note that there $(L-1)$ rows of all 0's below the top row. Then,

$$x(t+1) = Mx(t) \quad (1)$$

We can also consider M as a block matrix composed of K rows and K columns

of $L \times L$ matrices.

$$M = \begin{bmatrix} B_1 & \cdots & B_{K-1} & B_K \\ Q_1 & & & \\ & \ddots & & \\ & & Q_{K-1} & 0 \end{bmatrix} \quad (2)$$

where

$$Q_i = \begin{bmatrix} q_{i11} & \cdots & q_{iL1} \\ \vdots & & \vdots \\ q_{i1L} & \cdots & q_{iLL} \end{bmatrix}, B_i = \begin{bmatrix} b_{i1} & \cdots & b_{iL} \\ 0 & \cdots & 0 \\ \vdots & & \vdots \\ 0 & \cdots & 0 \end{bmatrix} \quad (3)$$

Observe that in block form M looks like the Leslie matrix. Likewise, we can consider $\mathbf{x}(t)$ as a block vector.

$$\mathbf{x}(t) = \begin{bmatrix} \mathbf{x}_1(t) \\ \vdots \\ \mathbf{x}_K(t) \end{bmatrix} \quad (4)$$

where

$$\mathbf{x}_i(t) = \begin{bmatrix} x_{i1}(t) \\ \vdots \\ x_{iL}(t) \end{bmatrix} \quad (5)$$

3 Results

Let l_{ij} be the probability an organism in state $(1, 1)$ reaches state (i, j) . There may be several ways an organism can reach state (i, j) . For example, one way to reach state $(3, 2)$ is to go from state $(1, 1)$ to $(2, L)$ to $(3, 2)$. There may also be *no* way that an organism can reach state (i, j) (in which case $l_{ij} = 0$). Thus,

$$l_{ij} = \sum_{s \in S_{ij}} \text{probability of staying on path } s \quad (6)$$

where S_{ij} is the set of *all* paths from $(1, 1)$ to (i, j) . Let us define more explicitly the notion of a path from $(1, 1)$ to (i, j) . In words, a path (a) begins at state $(1, 1)$, (b) ends at state (i, j) , (c) leaves every state it enters (except state (i, j)), and (d) takes $(i - 1)$ steps to get there. More explicitly:

A set Q represents a path from $(1, 1)$ to (i, j) iff Q satisfies the following.

(a) exactly one of $q_{1,1,1}, q_{1,1,2}, \dots, q_{1,1,L} \in Q$

(b) exactly one of $q_{i-1,1,j}, q_{i-1,2,j}, \dots, q_{i-1,L,j} \in Q$

(c) $\forall (x, y, z) \neq (i - 1, y, j), q_{x,y,z} \in Q \Rightarrow$ exactly one of $q_{x+1,z,1}, q_{x+1,z,2},$

$\dots, q_{x+1,z,L} \in Q.$

(d) $|Q| = i - 1$

$$\begin{bmatrix} b_{11} - \lambda & b_{12} & b_{13} & b_{21} & b_{22} & b_{23} & b_{31} & b_{32} & b_{33} & b_{41} & b_{42} & b_{43} \\ 0 & -\lambda & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & -\lambda & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ q_{111} & q_{121} & q_{131} & -\lambda & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ q_{112} & q_{122} & q_{132} & 0 & -\lambda & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ q_{113} & q_{123} & q_{133} & 0 & 0 & -\lambda & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & q_{211} & q_{221} & q_{231} & -\lambda & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & q_{212} & q_{222} & q_{232} & 0 & -\lambda & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & q_{213} & q_{223} & q_{233} & 0 & 0 & -\lambda & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & q_{311} & q_{321} & q_{331} & -\lambda & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & q_{312} & q_{322} & q_{332} & 0 & -\lambda & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & q_{313} & q_{323} & q_{333} & 0 & 0 & -\lambda \end{bmatrix}$$

Figure 3: Sample transition matrix $M - \lambda I$ with $K = 4, L = 3$

3.1 Eigenvalues and Eigenvectors

Theorem 1 *The characteristic equation of M (defined by $Mx = \lambda x$) is*

$$\sum_{i=1}^K \sum_{j=1}^L \frac{b_{ij} l_{ij}}{\lambda^i} = 1 \quad (7)$$

Figure 3 is a sample transition matrix $M - \lambda I$ with $K = 4, L = 3$. The reader, in following the proof, may find it useful to refer to this matrix as an example.

Proof. Observe that:

1. b_{ij} is at row 1, column $(i-1)L + j$ of M
2. q_{ijk} is at row $iL + k$, column $(i-1)L + j$ of M

Let $M' = M - \lambda I$. The row and column of an element will now always specify the location of that element in M' . Expand M' about the top row.

$$\det(M') = (-\lambda)^{KL} + \sum_{i=1}^K \sum_{j=1}^L (-1)^{N-1} b_{ij} \det(A_N) \quad (8)$$

where $N = (i-1)L + j$ (the column index of b_{ij}) and A_N is the $(KL-1) \times (KL-1)$ submatrix of M' obtained by deleting the N th row and N th column of M' .

$$\det(A_N) = (-\lambda)^{KL-N} \det(B) \quad (9)$$

where \mathbf{B} is an $(N-1) \times (N-1)$ submatrix of \mathbf{M}' (rows 2 through N , columns 1 through $N-1$). A standard definition of the determinant is used in calculating $\det(\mathbf{B})$.

Definition: Let $\mathbf{A} = [a_{ij}]$ be an $n \times n$ matrix. Then

$$\det(\mathbf{A}) = \sum \pm a_{1j_1} a_{2j_2} \cdots a_{nj_n} \quad (10)$$

where the summation ranges over all permutations $j_1 j_2 \cdots j_n$ of the set $S = \{1, 2, \dots, n\}$. The sign is positive if the permutation $j_1 j_2 \cdots j_n$ has an even number of inversions, odd otherwise.

I will take a *permutation* of a matrix \mathbf{A} ($n \times n$) to mean a set of n elements of \mathbf{A} such that no two of them are in the same row or column. A non-zero permutation is one with no zero elements. Hence,

$$\det(\mathbf{A}) = \sum_{P \in \mathcal{P}} \pm \prod_{s \in P} s \quad (11)$$

where \mathcal{P} is the set of all permutations of \mathbf{A} .

Consider a non-zero permutation P of \mathbf{B} . Elements in P will be either some q_{xyz} or $-\lambda$. To keep track of which $-\lambda$'s are which, denote λ_t to be the λ at row t , column t . Divide P into two sets, $P = P_q \cup P_\lambda$, where

$$P_q = \{q_{xyz} | q_{xyz} \in P\}$$

$$P_\lambda = \{\lambda_t | \lambda_t \in P\}$$

Definition: A permutation P represents a path from $(1, 1)$ to (i, j) iff P_q represents a path from $(1, 1)$ to (i, j) .

Claim 1: Every path from $(1, 1)$ to (i, j) is represented by a unique, non-zero permutation of \mathbf{B} .

Suppose we are given a path from $(1, 1)$ to (i, j) . We want to find a permutation of \mathbf{B} that represents this path. Since the elements in a path all have different age components, it is easy to see that the corresponding elements in \mathbf{B} have no rows or columns in common. Since there are $(i-1)$ such elements, it suffices to find $(N-1) - (i-1)$ other non-zero elements in \mathbf{B} with no rows or columns in common with these or with each other. The other elements in the permutation must be $-\lambda$'s (otherwise, the permutation would not represent a path, by violation of property (d)).

Suppose the given path is represented by:

$$\{q_{11s_1}, q_{2s_1s_2}, q_{3s_2s_3}, \dots, q_{i-2, s_{i-3}, s_{i-2}}, q_{i-1, s_{i-2}, j}\}$$

These elements are in rows:

$$L + s_1, 2L + s_2, 3L + s_3, \dots, (i-2)L + s_{i-2}, (i-1)L + j$$

and in columns:

$$1, L + s_1, 2L + s_2; \dots, (i-3)L + s_{i-3}, (i-2)L + s_{i-2}$$

Observe that the row of one edge is equal to the column of the next edge. Also, there are $(N-2) - \lambda$'s in \mathbf{B} (which appear in every row and column of \mathbf{B} except column 1 and except row $N = (i-1)L + j$). Hence, there are $(N-2) - [(i-1) - 1] = (N-i) - \lambda$'s left which have no rows or columns in common with the elements of the path. Hence, we have found a permutation which represents the given path. Further, since there are *exactly* $(N-i) - \lambda$'s from which to choose $(N-i)$, this permutation is unique.

Claim 2: Every non-zero permutation P of \mathbf{B} represents a path from $(1, 1)$ to (i, j) (This is the converse of claim 1).

Suppose P is a non-zero permutation of \mathbf{B} . It suffices to show that P satisfies properties (a) through (d) (mentioned previously).

(a), (b) Exactly one non-zero element from column 1 is in P , and exactly one non-zero element from row N is in P . In \mathbf{B} , there is no $-\lambda$ in column 1 or in row N . The only elements in \mathbf{B} in column 1 are q_{111}, \dots, q_{11L} . The only elements in \mathbf{B} in row N are $q_{i-1,1,j}, \dots, q_{i-1,L,j}$.

(c) Suppose $q_{xyz} ((x, y, z) \neq (i-1, y, j)) \in P$. q_{xyz} is in row $xL + y$. Also, exactly one non-zero element of \mathbf{B} from column $xL + y$ is in P (but it cannot be λ_{xL+y} , because it is in row $xL + y$). The only other choices are $q_{x+1,y,1}, \dots, q_{x+1,y,L}$.

(d) We must show $|P_q| = i - 1$. Clearly, $\lambda_2, \dots, \lambda_L \in P$. Therefore, exactly one element of \mathbf{Q}_1 (equation (3)) is in P (namely q_{11d} for some d). This implies that $\lambda_{L+1}, \lambda_{L+2}, \dots, \lambda_{2L} \in P$, except λ_{L+d} . Therefore, exactly one element of \mathbf{Q}_2 is in P , and so on. Exactly one element of each $\mathbf{Q}_1, \dots, \mathbf{Q}_{i-1}$ is in P . So, $|P_q| = i - 1$.

Claim 3: The number of inversions in a non-zero permutation of \mathbf{B} is $(N-i)$.

Definition: the number of inversions in a permutation is the number of pairs of elements in the permutation for which $\text{column}(\text{elt1}) < \text{column}(\text{elt2})$, but $\text{row}(\text{elt1}) > \text{row}(\text{elt2})$.

Consider a non-zero permutation P . Observe that no two elements of P_q are inverted and no two elements of P_λ are inverted. Therefore, the only possible inversions occur between an element in P_q and an element in P_λ .

Consider some $\lambda_t \in P_\lambda$ (λ_t is at row t , column t , ($2 \leq t \leq N$)). We wish to find all elements $q_{xyz} \in P_q$ such that $\text{column}(q_{xyz}) < t$ and $\text{row}(q_{xyz}) > t$. Pick $q_{xyz} \in P_q$ such that $\text{column}(q_{xyz}) < t$, but for any other element $q_{abc} \in P_q$, if $\text{column}(q_{abc}) < t$, then $\text{column}(q_{abc}) < \text{column}(q_{xyz})$. Because there is at least one element in P_q whose column is less than t (that is, one element is at column $1 < 2 \leq t$), such a q_{xyz} can always be found.

Observe that $\text{row}(q_{xyz}) = \text{column}(q_{x+1,z,d})$, which by choice of q_{xyz} must be greater than t . So, q_{xyz} is inverted with λ_t . Using this observation (that in a

non-zero permutation of \mathbf{B} , the row of one element is the column of the next), it can be shown that no other elements in P_q are inverted with λ_t . Hence, every $\lambda_t \in P_\lambda$ is inverted with exactly one element $q_{xyz} \in P_q$. Therefore, the number of inversions of P is $|P_\lambda| = N - i$.

Claims 1, 2, and 3 prove a one-to-one, onto correspondence between non-zero permutations of \mathbf{B} and paths from $(1, 1)$ to (i, j) . From (11),

$$\det(\mathbf{B}) = \sum_{P \in \mathcal{P}} (-1)^{(N-i)} (-\lambda)^{N-i} \prod_{s \in P_q} s = \lambda^{N-i} l_{ij}$$

Substituting into (9),

$$\det(\mathbf{A}_N) = (-1)^{KL-N} \lambda^{(KL-N)+(N-i)} l_{ij}$$

Substituting into (8),

$$\begin{aligned} \det(\mathbf{M}') &= (-\lambda)^{KL} + \sum_{i=1}^K \sum_{j=1}^L (-1)^{(N-1)+(KL-N)} b_{ij} \lambda^{KL-i} l_{ij} = 0 \\ &\Rightarrow \sum_{i=1}^K \sum_{j=1}^L \frac{b_{ij} l_{ij}}{\lambda^i} = 1 \end{aligned}$$

Theorem 2 Consider $S = \{i | (1 \leq i \leq K), b_{ij} l_{ij} > 0 \text{ for some } 1 \leq j \leq L\}$. If the greatest common divisor of the elements in S is 1, then \mathbf{M} has a single positive, real eigenvalue and this eigenvalue is strictly greater in magnitude than all other eigenvalues of \mathbf{M} .

This result applies if, for example, $b_{25} > 0$, $b_{31} > 0$, all other $b_{ij} = 0$, and $l_{25} > 0$, $l_{31} > 0$, but not if $l_{25} = 0$ or $l_{31} = 0$. This result does not apply if, for example, $b_{21}, \dots, b_{2L} > 0$, $b_{41}, \dots, b_{4L} > 0$, and all other $b_{ij} = 0$.

Proof: Let

$$d_i = \sum_{j=1}^L b_{ij} l_{ij}$$

Note, $d_i > 0$ iff $i \in S$. Then, the characteristic equation is

$$\sum_{i=1}^K \frac{d_i}{\lambda^i} = 1$$

Observe the similarity to the characteristic equation of the Leslie matrix:

$$\sum_{i=1}^K \frac{b_i l_i}{\lambda^i} = 1$$

It has been shown for the Leslie matrix L that if the greatest common divisor of $\{i|b_i > 0\}$ is 1 (note that l_i always > 0), then L has a real, positive eigenvalue that is largest in magnitude. The proof that this result is true when $\text{g.c.d.}\{i|d_i > 0\} = 1$ is identical (see Cull, 1973, pp. 649-650 or Getz and Haight, 1989, pp. 40-42).

An extension of the *age-stage* model is to let organisms be born into *all* stage classes (not just stage 1). In this way, some type of genetic structure can be built into the model. For example, large organisms might give birth to large children, and small organisms might give birth to small children. A simple example shows that the previous results do not apply. Consider a population with 1 age class and 2 size classes. Suppose all organisms in stage 1 give birth to 1 child in stage 1, and all organisms in stage 2 give birth to 2 children in stage 2. Then,

$$M = \begin{bmatrix} 1 & \\ & 2 \end{bmatrix}$$

The characteristic equation does not satisfy theorem 1. Also, M has more than one real, positive eigenvalue.

The eigenvector associated with the dominant eigenvalue can be found. This eigenvector gives the distribution of the population which is approached asymptotically. Consider M' as a block matrix composed of K rows and K columns of $L \times L$ matrices.

$$M' = \begin{bmatrix} B_1 - \lambda I & B_2 & \cdots & B_K \\ Q_1 & -\lambda I & & \\ & \ddots & \ddots & \\ & & Q_{K-1} & -\lambda I \end{bmatrix} \quad (12)$$

where B_i, Q_i are given by (3). Also, consider $x(t)$ as a block vector given by (4) and (5). An eigenvector satisfies

$$M'x(t) = 0$$

Multiplying out the top row gives

$$\sum_{i=1}^K B_i x_i(t) = \lambda I x_1(t) \quad (13)$$

This implies that x_{11} is unconstrained and all other $x_{1j} = 0$. Multiplying out the other rows gives

$$Q_{i-1} x_{i-1}(t) - \lambda I x_i(t) = 0 \quad (14)$$

$$\Rightarrow x_i(t) = \frac{Q_{i-1} x_{i-1}(t)}{\lambda} = \frac{Q_{i-1} Q_{i-2} \cdots Q_1}{\lambda^i} x_1(t) \quad (15)$$

Let $x_{11} = 1$. Then, from (15)

$$x_{ij} = \frac{l_{ij}}{\lambda^i} \quad (16)$$

The stable population distribution decays exponentially with age (as it does in the Leslie model).

3.2 Harvesting

Beddington and Taylor (1973) proved that the optimal harvesting policy for the Leslie model involves partial harvesting of one age class and complete removal of another (thus reducing the maximum age of the population). An optimal harvesting policy is defined to be a policy which harvests the greatest percentage of the *total* population while maintaining equilibrium.

A similar result holds for the *age-stage* model. Suppose allowable harvesting policies consist of removing a fixed percentage ($0 \leq h_i \leq 1$) of organisms from each *age* class. Then, it can be shown, using Theorem 1 and an argument identical to Beddington and Taylor's, that the optimal harvesting policy for the *age-stage* model involves partial harvesting of one age class and complete removal of another.

However, this is not a very interesting result, since, as stated earlier, it may be difficult to harvest a population based upon the *age* of organisms. A more interesting question considers the effects of harvesting a fixed percentage ($0 \leq h_j \leq 1$) of organisms from each *stage* class.

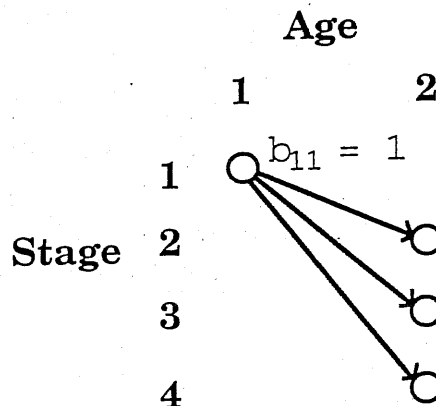


Figure 4: Counter-example for *age-stage* model

A simple counter-example shows that harvesting two stage classes is not always optimal. Consider a population modelled by the graph in figure 4. Suppose each organism in state (1, 1) gives birth to 1 organism ($b_{11} = 1$, all other $b_{ij} = 0$). Then, the optimal policy harvests all of stages 2, 3, and 4.

The same problem was investigated for the *age-size* model. This model is more similar in structure to the Leslie model in the sense that organisms progress through size/age classes in sequential order and cannot skip between stages. This property might lend the model to a proof (similar to Beddington and Taylor's) that two-stage harvesting is optimal. However, no proof nor any counter-example was found.

References

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