The Age-Stage, Two-Sex Life Table with an Offspring Sex Ratio Dependent on Female Age

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Abstract

In the age-stage, two-sex life table, both sexes and variable developmental rates are incorporated into life table theory. However, in many species, the sex ratio of the offspring depends on the age of the female. Thus, the sex ratio based on the pooled total fecundity of a single cohort may lead to an over- or under-estimation of population parameters and consequently to errors in simulation. This paper describes a new theoretical approach in which the female age dependence of the offspring sex ratio is recognized. The population parameters (the intrinsic rate of increase, the net reproductive rate, and the mean generation time) and the sex ratio of a population with a stable age structure can be calculated with this new theory.

Key words: Life table, Sex ratio, Female age.

Introduction

Most demographic theories concern only one sex, which is typically the female. Most animals are, however, bisexual. Sexual dimorphism in development and survivorship is commonly observed in these animals. Chi and Liu [(9)] developed the age-stage, two-sex life table theory incorporating both sexes and a variable developmental rate among individuals. A detailed discussion on raw data analysis based on the age-stage, two-sex life table is presented by Chi [(5, 6)]. An application of the theory to problems of mass rearing and harvesting is reported by Chi and Getz [(11)] and Chi [(8)]. The theory has also been applied to the timing of pest management [(7)]. During the past few years, the age-stage, two-sex life table has been used in many studies. For example, more than 10 papers on the topic have been published since 2010 [(1, 2, 16, 18, 19, 25, 26, 29, 31, 32, 33)]. Pollak [(24)] and Caswell and Weeks [(4)] also discussed the

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importance of the two-sex problem. In all two-sex models, however, the sex ratio of the offspring may be included as a variable in addition to the survival rate, developmental rate, and fecundity. It has been reported that the offspring sex ratio depends on the female age [15, 17, 23, 28]. Because both sexes and the variable sex ratio of the offspring are critical in demography, the traditional female age-specific life tables [3, 20, 21, 22] are insufficient in most cases. If the offspring sex ratio varies significantly among different-aged females, not only the theory of population growth but also the population projection should recognize this variation. Expanded from the age-stage, two-sex life table theory [9], a new theory including a variable sex ratio in the offspring depending on the age of the female is derived in this paper. A theoretical approach is emphasized, and the formulae for each parameter are given in the respective sections.

1. Age-stage-sex structure of population

Because the developmental rate may differ between the sexes, the age-stage structure of a population is defined as a three-dimensional matrix *N*. The first plane represents the female population (type F), the second plane represents the male population (type M), and the third plane represents those individuals that died before the adult stage (the unknown, type U). The element $n(i,j,x)$, of the matrix *N* is the number of individuals of age *i*, stage *j*, and sex *x*. For example, $n(4,3,1)$ is the number of female individuals of age 4 and stage 3, $n(5,2,2)$ is the number of male individuals of age 5 and stage 2, and $n(4,2,3)$ is the number of individuals of type U of age 4 and stage 2 (they will die before they reach the adult stage). Matrix *N* describes the growth, development, and fecundity of each type separately.

2. Age-stage-specific growth rate, developmental rate, and fecundity

Based on matrix *N*, each sex has its own age-stage-specific growth rate, developmental rate, and fecundity. The age-stage-specific growth rate (matrix *G*), developmental rate (matrix *D*), and fecundity (matrix *F*) are the fundamental data of the life table. These quantities can be obtained by tracing the life history of a newborn cohort from birth to death. Because a variable sex ratio is included, the offspring produced daily by an individual female must be reared to the adult stage in separate cages. The number of offspring of each sex is recorded when they emerge as adults. Furthermore, the life history data must be analyzed for each sex separately, using the concept described by Chi [5], to obtain matrices *G*, *D*, and *F*. The analytical results are placed in three matrices: the growth rate matrix *G*, the developmental rate matrix *D*, and the fecundity matrix *F*. In matrix *G*, the element $g(i,j,x)$ is the probability that an individual of age i, stage j, and sex x will grow to age i+1 but remain in stage j after one age interval (assuming sex change is impossible). In matrix D, the element $d(i,j,x)$ is the probability that an individual of age i, stage j, and sex x will develop to stage j+1 and age i+1 after one age unit. In matrix F, element $f(i,j,x)$ is the number of offspring of sex x produced by a female of age i and stage j, i.e., $n(i,j,1)$. The different numbers of elements in matrices G, D, and F imply the different developmental durations in each stage for the two sexes. Because the type U individuals will not develop to the adult stage, the elements of the developmental rate matrix D are all zero for the stage of type U immediately preceding the adult stage.

3. Population growth

Based on the concept presented by Chi and Liu [9], the process of population growth can be represented with the following calculations: the daily newborns of each sex x, $n(0,1,x)$, can be calculated as

$$n(0,1,x) = \sum_{i=1}^{n}\sum_{j=1}^{m} n(i,j,1)\cdot f(i,j,x) \qquad (1)$$

Equation 1 explicitly states that a newborn female will not produce offspring, i.e., the element $n(0,1,1)$ does not appear on the right-hand side; moreover, all offspring are produced by females. Because the remaining elements of the first column (the first life stage) are the survivors of $n(0,1,x)$, we calculate them as

$$n(i,1,x) = n(i-1,1,x)\cdot g(i-1,1,x) \qquad (2)$$

The column immediately preceding the last column, i.e., the column representing the change from the second life stage (the larval stage) to the last life stage (the adult), can be calculated sequentially as

$$n(i,j,x) = n(i-1,j,x)\cdot g(i-1,j,x) + n(i-1,j-1,x)\cdot d(i-1,j-1,x) \qquad (3)$$

The total number of individuals of age i in the population is the summation of individuals of the same age but different stage and sex. This number can be calculated as

$$A(i) = \sum_{j=1}^{m}\sum_{x=1}^{3} n(i,j,x) \qquad (4)$$

Similarly, the total number of individuals of stage j in the population is the summation of individuals of the same stage but different age and sex. This number can be calculated as

$$B(j) = \sum_{i=0}^{n}\sum_{x=1}^{3} n(i,j,x) \qquad (5)$$

The total number of individuals of sex x is the summation of all individuals of the same sex but different age and stage. This number can be calculated as

$$C(x) = \sum_{i=0}^{n}\sum_{j=1}^{m} n(i,j,x) \qquad (6)$$

The sex ratio is then

$$F:M:U = C(1):C(2):C(3) = \sum_{i=0}^{n}\sum_{j=1}^{m} n(i,j,1) : \sum_{i=0}^{n}\sum_{j=1}^{m} n(i,j,2) : \sum_{i=0}^{n}\sum_{j=1}^{m} n(i,j,3) \qquad (7)$$

4. Age-stage-specific survival rate for each sex

In Chi and Liu's model [9], both sexes are combined before the adult stages. If the sex ratios of the offspring produced by females of different ages are known, we can calculate the age-stage-specific survival rate for each sex separately, as Getz and Haight [14] suggested. The survival matrix S can be obtained with an approach similar to that used for population growth as follows:

First, we set $s(0,1,x) = 1$. We then calculate the remaining elements of the first stage as

$$s(i,j,x) = s(i-1,j,x) \cdot g(i-1,j,x) \qquad (8)$$

We then calculate the elements of the remaining columns (the second to the last life stages) as

$$s(i,j,x) = s(i-1,j,x) \cdot g(i-1,j,x) + s(i-1,j-1,x) \cdot d(i-1,j-1,x) \qquad (9)$$

Because individuals of different sexes may have different developmental rates and growth rates, the different sexes may have different age-stage-specific survival rates.

5. Intrinsic rate of increase

Because the number of females determines the number of offspring of each sex, the intrinsic rate of increase r can be calculated as follows:

$$\sum_{i=0}^{n} e^{-r(i+1)} \sum_{j=1}^{m} s(i,j,1) \cdot f(i,j,1) = 1 \qquad (10)$$

The finite rate can be calculated as $\lambda = e^r$. Note that although we used only the female population to calculate the intrinsic rate, this approach differs from the traditional female age-specific life table because we retain the advantage of age-stage structure. This characteristic is important because it implies that we can incorporate the variable developmental rate correctly.

6. Stable age-stage distribution of female population

As time approaches infinity and the matrices G, D, and F remain constant, the population will approach a stable age-stage-sex distribution and will increase at a constant growth rate λ ($\lambda = e^r$). This asymptotic behavior also implies that the number of individuals in each age-stage group will increase λ-fold after one age unit. The stable age-stage distribution of the female population can then be obtained. Initially, we let the first age-stage group of females be unity. This choice means that $p(0,1,1) = 1$. We then calculate the remaining elements of stage one as

$$p(i,j,1) = \frac{p(i-1,j,1) \cdot g(i-1,j,1)}{\lambda}$$

(For $j = 1$ and $i > 0$). (11)

After all elements of the first stage are known, we can calculate the elements of the subsequent stages as

$$p(i,j,1) = [p(i-1,j,1) \cdot g(i-1,j,1) + p(i-1,j-1,1) \cdot d(i-1,j-1,1)]/\lambda \qquad (12)$$

This expression gives the stable age-stage distribution of the female population under the assumption that $p(0,1,1) = 1$.

7. Stable age-stage-sex distribution

Given the stable age-stage distribution of the females at time *t*, we can calculate the newborn females (F_N), males (M_N), and U-types (U_N) at time $t+1$ as

$$F_N = \sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,1)\cdot f(i,j,1) = \lambda \qquad (13)$$

$$M_N = \sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,1)\cdot f(i,j,2) \qquad (14)$$

$$U_N = \sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,1)\cdot f(i,j,3) \qquad (15)$$

The ratio of male newborns to female newborns in the stable age-stage distribution can be calculated as

$$\alpha = \frac{\sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,1)\cdot f(i,j,2)}{\sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,1)\cdot f(i,j,1)} \qquad (16)$$

The ratio α is the stable age-stage distribution of the males in comparison to that of the females. Similarly, the ratio of U-type newborns to female newborns can be calculated as

$$\beta = \frac{\sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,1)\cdot f(i,j,3)}{\sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,1)\cdot f(i,j,1)} \qquad (17)$$

The ratio β is the stable age-stage distribution of the U type in comparison with the females.

The total population size at time $t+1$ is

$$A = \sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,1) + \sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,2)\cdot\alpha + \sum_{i=0}^{n}\sum_{j=1}^{m} p(i,j,3)\cdot\beta \qquad (18)$$

where $p(i,j,2)$ and $p(i,j,3)$ are the stable age-stage distributions of type M and U calculated following similar procedures of female (Equations 11 and 12). The proportion of individuals of each age-stage-sex unit in the stable distribution is

$$q(i,j,x) = \frac{p(i,j,x)}{A} \qquad (19)$$

The proportion of age *i* in the stable age-stage-sex distribution is then

$$A_s(i) = \sum_{j=1}^{m}\sum_{k=1}^{3} q(i,j,k) \qquad (20)$$

The proportion of stage *j* in the stable age-stage-sex distribution is

$$B_s(j) = \sum_{i=0}^{n}\sum_{k=1}^{3} q(i,j,k) \qquad (21)$$

The proportion of sex *x* in the stable age-stage-sex distribution can be calculated as

$$C_s(x) = \sum_{i=0}^{n}\sum_{j=1}^{m} q(i,j,x) \qquad (22)$$

8. The age-stage-sex life expectancy

The life expectancy for individuals in different age-stage-sex units can be calculated as

$$E(i,j,x) = \frac{\sum_{k=i}^{n}\sum_{y=j}^{m} s'(k,y,x)}{s(i,j,x)} \qquad (23)$$

where $s'(k, y, x)$ is derived by assuming $s'(i, j, x) = 1$ and using matrices *G* and *D* as described by Chi and Liu [9] and Chi and Su [10]. Because individuals of the same age but different stage or sex may have different expectations of life, the age-stage expectation can reveal such differences and is therefore more precise than the traditional female age-specific life table.

9. The age-stage-specific reproductive value

Based on the concept of reproductive value [13], the age-stage specific reproductive value of female can be obtained as follows:

$$R(i,j,1) = \frac{e^{-r(i+1)}}{s(i,j,1)} \cdot \sum_{k=i}^{n} e^{-r(k+1)} \times \left[\sum_{y=j}^{m} s'(k,y,1) \cdot f(k,y,1)\right] \quad (24)$$

where $s'(k, y, 1)$ can be derived by the same method described in the previous section. This age-stage-specific reproductive value again reveals the possible differences among female individuals of the same age but different stage.

Conclusions

Most demographic theories concern only the female; however, many examples reveal the importance of the two-sex problem [12, 27, 30]. Studies on the two-sex model have revealed additional characteristics of bisexual populations [4, 9]. However, the female-age dependence of the offspring sex ratio is one of the problems requiring consideration for constructing the two-sex model and before treating nonlinear sex ratio problems. The variation in the offspring sex ratio according to the female age alters the sex ratio of the population over time as well as the growth rate of the population. If the offspring sex ratio remains constant in all female age groups, the results will be the same as those found with the original model developed by Chi and Liu [9]. However, if the sex ratio varies with the female age, the new age-stage-sex model provides a precise way to calculate the intrinsic rate of increase, the stable sex ratio, and the stable age-stage-sex structure. These quantities will not be correctly calculated by any two-sex model without an age-dependent sex ratio. Thus, the age-stage-sex model offers several advantages. It represents both sexes, incorporates the variable developmental rate, and addresses the female-age dependent offspring sex ratio. This paper outlines the theoretical framework and related formulae for an age-stage-sex model. Based on this framework, statistical analyses, simulations, and further development of the nonlinear model can be studied.

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