Advances in theory, data analysis, and application of the age-stage, two-sex life table for demographic research, biological control, and pest management

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With 12 figures

Abstract: This paper reviews and introduces innovative research pertaining to the age-stage, two-sex life table. The main topics discussed are: (1) Analysis of data involving group-reared life table studies. We address the rationale behind the data analysis used when constructing a group-reared life table. Proper analysis of grouped-reared life table data enables the collection of realistic and applicable data for ecological studies, devising efficient mass-rearing programs and formulating pest management routines using time- and labor-saving group-rearing methods. (2) The bootstrap-match technique. This novel technique is applicable to those instances when constructing a complete life table involves collecting the immature independently from the adult data. (3) Application of the set theory in life table research. This procedure enables a mathematical description of the population structure and bootstrap samples. (4) Application of the multinomial theorem. Using the multinomial theorem enables calculation of the exact probability of bootstrap samples. (5) Inclusion of infertile bootstrap samples. Because it is impossible to calculate the intrinsic rates of increase for infertile samples, they are normally omitted in life table analysis. Inclusion of these infertile bootstrap samples produces an unbiased life table analysis. (6) The Cartesian product. The Cartesian product of two sets produces the complete coverage of all possible differences. We compared the paired bootstrap test, the Cartesian paired test based on bootstrap results, and the Cartesian paired test based on the multinomial theorem. (7) Integration of life table data with predation data. This procedure, which is especially relevant to biological control programs, enables a comprehensive study of the predator-prey relationship. (8) Computer simulation based on life tables. Population projection based on the age-stage, two-sex life table not only provides the means to predict the dynamics of stage structures of a given pest population, but also provides an insight into the dynamics of predation capacity of the predator population. (9) Problems in life table research. Each of the subjects discussed is crucial for the theoretical advancement and practical applications of scientific demographic research.

Keywords: group-reared life table, bootstrap-match technique, set theory, multinomial theorem, Cartesian paired test, computer simulation, predation, infertile bootstrap sample

1   Introduction

Seventy years after Ernest Haeckel coined the term "Oecologie" (Haeckel 1866), Bodenheimer (1938) stated that animal ecology was a young science. Eighty years later, Chi et al. (2022a) claimed, once again, that "Ecology is still a young science", based on the fact that the majority of current ecological publications are primarily descriptive science. Evidence of insect metamorphosis has been dated as far back as the 300 Ma (millions of years) – eons before human culture (Belles 2011). Because the process of simplification has often been the "norm" of most scientific endeavors in the past, the description of insect life tables has been simplified for the past several decades to include only age-specific life tables that are based solely on the females of a given population. Unfortunately, this oversimplification has completely overlooked the important existence of their metamorphosis as well as the entire male population of the species being studied. The age-stage, two-sex life table theory is capable of explaining the stage differentiation (i.e., metamorphosis) as well as the differences in developmental rates among indi-

viduals in a mathematical procedure and calls attention to the variable adaptability of different developmental stages in insect population ecology. Obtaining a scientifically accurate and comprehensive analysis of the life table data for arthropod populations is just the beginning – life table results can be applied to research involving population interactions (e.g., predator-prey relationship) and management of populations (e.g., chemical and biological control of pest populations). Even since its initial introduction (Chi & Liu 1985), the age-stage, two-sex life table and its accompanying programs, i.e., TWOSEX-MSChart, CONSUME-MSChart, and TIMING-MSChart, have been widely used in entomological research during the ensuing two decades.

The age-stage, two-sex life table has been applied to numerous research fields: e.g., population fitness under constant and fluctuating temperatures (Wang et al. 2014, Bayu et al. 2017, Rismayani et al. 2021), demographic comparison of mites reared on different plant cultivars (Azadi Dana et al. 2018a,b), effect of inbreeding on population fitness (Peng et al. 2015), insect fitness on original and marginal hosts (Yang et al. 2021), how gene expression affects the tempera-

ture adaptability of insects (Zhou et al. 2022), effect of nutrition on population parameters of parasitoids (Wang et al. 2022), pesticide resistance of insect populations (Zhu et al. 2021), fitness of parasitoids reared on different host species (Zhao et al. 2021), the optimal ingredients in insects' diets (Xue et al. 2023), the contribution of diapausing individuals to population growth (Lin et al. 2023), and others.

Chi et al. (2020) gave an overview of the age-stage, two-sex life table, including the basic theory, data analysis, and applications, although many advanced subjects were not included in that review. Herein, the advanced, innovative or difficult theories, data analyses, and applications of the age-stage, two-sex life table are presented. As Kingland (1991) pointed out the importance of mathematics in ecological research, we will discuss in this review, the necessity of employing set theory, multinomial theorem, and Cartesian product as innovative techniques in modern life table research.

The collection of data needed to construct individually reared life tables is a time- and labor-consuming task. Chang et al. (2016) used a group-reared life table to study the demography of *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae). The group-reared life table is an interesting and important subject of insect demography and the data it provides can be analyzed using the TWOSEX-MSChart program (Chi 2023c). However, there are some difficulties that may be encountered and will need to be addressed.

In order to construct complete life tables for insects with an overwintering or dormancy period, Amir-Maafi et al. (2022) introduced the bootstrap-match technique. This method can be also used for insects that are difficult to mate in the laboratory or when the data needed for the immature and adult life tables are, by necessity, collected separately. We will discuss additional instances where the bootstrap-match technique can be applied.

Bootstrap is an important technique in numerous research fields (Efron & Tibshirani 1993). However, since bootstrap is completely based on computer-intensive simulation, Zhao et al. (2021) and Ding et al. (2021) used the multinomial theorem. Later, Chi et al. (2022b) used the set theory to describe the population composition and to calculate the fertile and infertile bootstrap samples. In the bootstrap technique, the paired bootstrap test, which is based on confidence intervals of differences between treatments, has been used as a reliable and precise method (Hesterberg et al. 2003, Wei et al. 2020). For a more complete comparison, Chi et al. (2022b) introduced the Cartesian paired test by using the set theory and Cartesian product.

Life tables are not only an important basis for a comprehensive understanding of population ecology of insects and mites, but because they are also a fundamental basis of successful mass-rearing when used to assess the impact of population-level effects (Chi and Getz 1988), different environmental conditions, and/or stressors, they are also important to the success of biological control and integrated pest management programs. Since the susceptibility of pests and natural enemies to pesticides varies with their stage, Chi (1990) noted that the timing of pest management based on the stage structure of pest populations is essential for successful control. Furthermore, Huang et al. (2018) introduced the estimation of uncertainty of computer simulation and its application to life table studies. Merging life table data with predation rate in computer simulation allows the prediction of pest population growth under the pressure exerted by one or more predators (Ding et al. 2021). A similar rationale can be used to test the effect of other stressors or control agents on selected insect species.

For informative purposes, we will include additional detailed reasoning and explanations on several other important topics, as well as discussing some common problems and mistakes in life table research, modelling, and statistics.

2   Group-reared life tables

Most entomological life table data have been traditionally collected by individually rearing the population individuals involved in the study; i.e., the individually-reared method. The advantages of individual-rearing include: (i) the detailed developmental duration of each individual and daily fecundity of each female adult can be obtained; (ii) the bootstrap technique, as well as the paired bootstrap test, can be easily applied to estimate the variances and standard errors of all parameters. The disadvantages of individual-rearing are: (i) it is generally time- and labor-consuming to record the detailed data for each individual; (ii) the effect of density is ignored; (iii) every insect has only a single mate paired by the researcher. If the mated female or male has been injured or has been weakened, it will not have an opportunity to pair with another mate. In contrast to the disadvantages of individual-rearing, group-rearing does offer several advantages: (i) it can save substantial time, labor, and space, thus reduce the rearing cost; (ii) females can mate with vigorous males and the probability that a female does not produce eggs due to being paired with a substandard mate is lowered; (iii) in group-rearing, insects can help others in ingesting and digesting their food (particularly true for some dipterans); (iv) in group-reared colonies, the growth of bacteria may be limited; e.g., Fonseca-Muñoz et al. (2019) demonstrated the bactericidal activity of larval excretions of *Chrysomya rufifacies* (Macquart) and *Cochliomyia macellaria* (Fabricius) (Diptera: Calliphoridae). A major disadvantage of group-rearing is that obtaining detailed data for each individual is impossible. Lacking data for each individual, it is not possible to apply the bootstrap technique to estimate the uncertainty of population parameters. This will be discussed later. Other possible disadvantages are: (i) if the colony is infected with bacteria or virus, the colony may collapse; (ii) crowding in preadult stages often decreases the growth rates and lowers the fecundity, especially in Lepidoptera larvae (Cerutti

et al. 1992); (iii) there may be cannibalism in group-rearing. However, if cannibalism is present in a natural setting, it can be revealed in the group-reared life table data.

Data generated by group-reared life tables may contribute to understanding the true population characteristics needed to instigate successful pest management practices; for example, in mass-rearing of agricultural pests for use in the sterile insect technique (Chang et al. 2016), or for generating the large number of medically important insects such as *Anopheles stephensi* Liston (Diptera: Culicidae) (Fazeli-Dinani et al. 2022) that may be required in some research projects. Li et al. (2021) compared the life tables of group- and individually-reared populations of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). They observed a higher intrinsic rate of increase (r) and finite rate of increase (λ), as well as a higher net reproductive rate (R_0) for thrips in the group-reared life table cohort than in individually-reared thrips. Conversely, Wang et al. (2021) reported that the life table parameters of group-reared *Ephestia elutella* (Hübner) (Lepidoptera: Pyralidae) were reduced on both artificial diets and tobacco leaves. Many factors may affect life tables, e.g., density, rearing medium, etc. In order to detect the genuine population parameters, individual- or group-rearing must be justified based on the biology of the insects being studied.

In the following sections, the shorter terms "intrinsic rate" and "finite rate" will be used.

2.1 Rationales for using group-reared life table data analysis

If the life table study is initiated with $n_{0,1}$ newborn individuals, the daily number of surviving insects and their stages can be recorded, i.e., n_{xj}, where x is age and j is stage. This is the matrix N showing the surviving number and stage differentiation of the life table cohort at age (time) x (Fig. 1). To clearly express subscripts when there are two number indices in the subscript of a variable, it is written with a comma separating the two (e.g., $n_{0,1}$). When there are two simple alphabetical indices (e.g., x as age and j as stage) in the subscript of a variable, it is written as n_{xj} without the comma.

According to Chang et al. (2016), the age-stage specific survival rate s_{xj} (the elements of matrix S) (Fig. 1) can be calculated as

$$s_{xj} = \frac{n_{xj}}{n_{0,1}} \tag{2.1}$$

In a similar fashion, the daily total number of eggs laid by all female adults is recorded, i.e., $f_{x,total}$ at age x (Fig. 2). The data $f_{x,total}$ is actually the element of matrix F_{total} which can be used to calculate the age-stage specific fecundity f_{xj} (matrix F) as

$$f_{xj} = \frac{f_{x,total}}{n_{xj}} \tag{2.2}$$

Fig. 1. The age-stage-specific survival rate matrix S is calculated from the matrix N of life table records by multiplying every n_{xj} with $1/n_{0,1}$ (E: egg, L: larva, P: pupa, F: female adult, and M: male adult.).

Fig. 2. The matrix F_{total} is the daily record of the total number of eggs laid by all female adults at age x; the age-specific fecundity of female adults is calculated using $f_{x,total}$ and n_{xj} of matrix N.

By using the data from s_{xj} and f_{xj}, the age-specific survival rate (l_x) and age-specific fecundity (m_x) can then be calculated as

$$l_x = \frac{\sum_{j=1}^{k} n_{xj}}{n_{0,1}} = \sum_{j=1}^{k} s_{xj} \tag{2.3}$$

$$m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}} = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{l_x} \tag{2.4}$$

where k is the number of stages. Based on the data of s_{xj}, f_{xj}, l_x, and m_x, the population parameters (i.e., R_0, r, λ, T, etc.) can be calculated according to Chi and Liu (1985) and Chang et al. (2016).

2.2 Group-reared life table data with predation/consumption rate

If the daily consumption of each age-stage unit is recorded with the group-reared life table data, the consumption matrix C and the net predation rate can be calculated (Fig. 3). According to Chi & Yang (2003), the net consumption rate (C_0) can be calculated as

$$C_0 = \sum_{x=0}^{\infty} \sum_{j=1}^{k} s_{xj} c_{xj} \qquad (2.5)$$

The transformation rate from prey population to predator offspring can be calculated as

$$Q_p = \frac{C_0}{R_0} \qquad (2.6)$$

2.3 Converting group-reared life tables to individually-reared life tables

To apply the bootstrap technique to estimate the standard errors of population parameters, and to obtain the matrices G, D, and F needed for population projection (Chi & Liu 1985, Chi 1990), it is necessary to convert the group-reared life table to an individually-reared life table. The conversion of a group-reared to an individually-reared life table is a complicated trial-and-error process. By using the TWOSEX-MSChart program (Chi 2023c), the group-reared life table with detailed stages, e.g., egg, larva, pupa, and adult (male and female), can first be converted to two-stage group-reared data (preadult and adult). The detailed preadult and adult duration data for each individual can then be constructed via trial-and-error methods. To simplify the conversion, three or four replicates of the group-reared life table study using a smaller cohort ($n = 10\sim20$)

can be used. The converted individual life tables of these replicates can be pooled to produce individually-reared life tables with more realistic variability. If the conversion of group-reared life table to individually-reared data is difficult or impossible, these three or four group-reared life tables can alternatively be used to estimate the mean and standard error through general statistics.

3 Bootstrap-match technique

In most life table studies, data are recorded for each individual of a cohort of insects from their birth to death. However, there are instances where continuous observation of individual insects is difficult or impractical. Amir-Maafi et al. (2022) developed the bootstrap-match technique to construct a life table for the sunn pest, *Eurygaster integriceps* Puton (Hemiptera: Scutelleridae). Wei et al. (2022) used a similar procedure to construct life tables of the egg parasitoid *Anastatus japonicus* Ashmead (Hymenoptera: Eupelmidae) reared on eggs of the Japanese giant silkworm (*Caligula japonica* Moore) (Lepidoptera: Saturniidae) and the Chinese oak silkworm (*Antheraea pernyi* Guérin-Méneville) (Lepidoptera: Saturniidae). They demonstrated that this parasitoid species could be efficiently reared on *A. pernyi* eggs, and could potentially be used as an effective biocontrol agent against *C. japonica*. Ullah et al. (2022c) used the bootstrap-match technique in their research on the life table of *Eotetranychus kankitus* Ehara (Acari: Tetranychidae) at different temperatures.

3.1 When can you apply the bootstrap match?
The bootstrap match can be used in the following situations: (1) When immature and adult life table data are collected
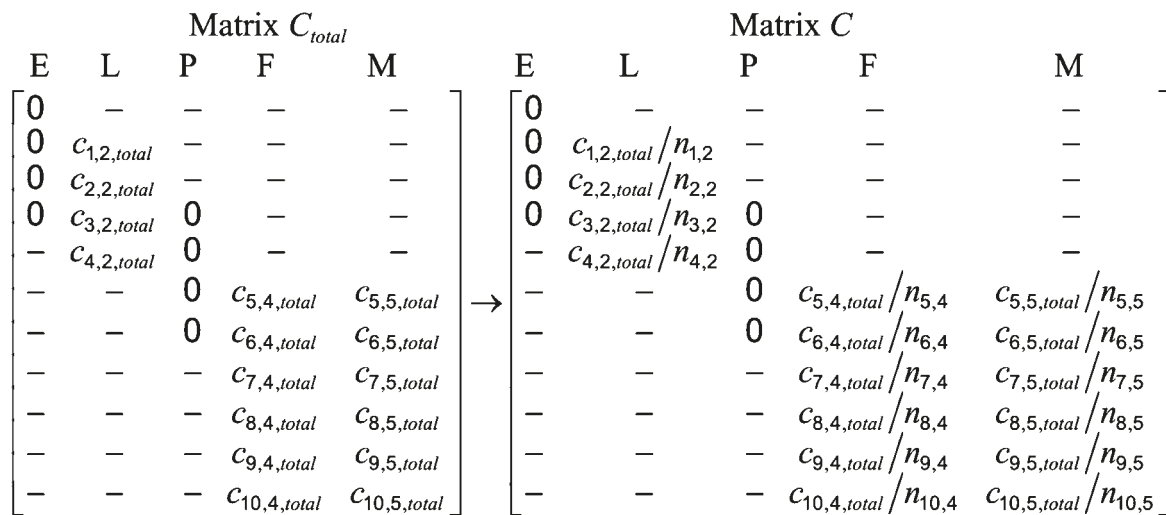

Fig. 3. The matrix C_{total} contains the daily record of total consumption (or predation) by all individuals n_{xj} at age x and stage j, i.e., $c_{x,j,total}$; the age-stage specific consumption rate matrix C is calculated using n_{xj} of matrix N.

separately due to obligatory diapause or dormancy. (2) Immature and adult life table data are collected independently due to difficulties in mating the adults in the laboratory. (3) A large cohort is used for collecting immature data, but a much smaller cohort is used for the adult data, e.g., insects having a short immature developmental period and an extended adult longevity. (4) Immature data were collected using individual-rearing while the adult data were obtained using group-rearing, or vice versa. (5) Hatched immatures from egg masses are used for development of an immature life table. (6) Researchers collect the immature and adult life table data simultaneously using different cohorts of insects. This latter practice is more efficient than collecting cohort life table data from birth to death, especially when an urgent study of newly emerged pests or invasive pests may be needed. In Fig. 4, there are 150 immature individuals and 30 adults in a hypothetical cohort.

Some insect species such as the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), produce egg masses. Separating eggs for individual-rearing would likely damage the eggs. If hatched first instars of a known egg duration are used in an immature life table study and the adult life table data are collected from a small sample of adults, the rationale of using bootstrap-match as in Amir-Maafi et al. (2022) and using viable eggs for the life table study conducted by Mou et al. (2015) can be integrated to construct a realistic life table.

3.2   Rationales of bootstrap-match technique

Regular life tables were split into immature and adult life tables by Amir-Maafi et al. (2022) to demonstrate the applicability of the bootstrap-match method. The rationales of using bootstrap-match can be seen when: (1) Lewontin (1965) and Akca et al. (2015) demonstrated that the preadult survival rate is a deterministic factor of life table parameters. By using a large cohort in the immature life table study, a more precise preadult survival rate can be obtained compared to using a smaller cohort in regular life table development. (2) The proportions of sexes (i.e., N_f/N, N_m/N, and N_n/N) are critical factors of population parameters which can be more precisely determined from the immature life table using a large cohort. (3) The mean fecundity of adult females is the same.

De Bona (2017) studied the effect of *Trypanosoma cruzi* Chagas (Euglenozoa: Trypanosomatida: Trypanosomatidae), the etiological agent of Chagas disease, on the life table of *Mepraia spinolai* (Porter) (Hemiptera: Reduviidae), a sylvatic vector of Chagas disease. In that study, 563 eggs were used to collect the immature (nymph) life table data from which 178 individuals (138 females and 40 males) emerged as adults. The adult longevity and fecundity data were collected for one year or longer using 50 adults (25 females and 25 males). The immature life table data (563 eggs) and adult life table data (50 adults) were then used to construct the composite life table based on the bootstrap-match technique.
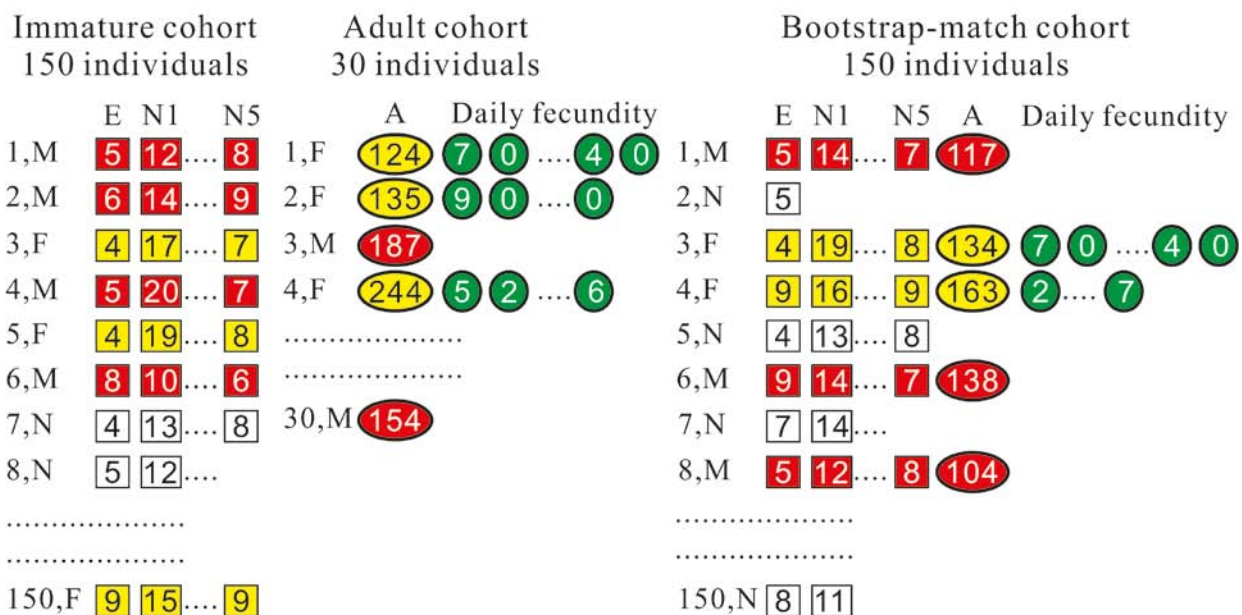
Fig. 4. Application of bootstrap-match technique to couple the life table of 150 immature individuals (E: egg, N1~N5: nymphal stages 1~5, F: female adult, M: male adult) with the adult life table derived from 30 adults. The numbers in the boxes are the developmental durations, the numbers in ovals are the adult longevities, and the numbers in the circles are the daily fecundities. Because data from only a few individuals from both the immature and adult cohorts are shown in the figure, the data from the bootstrap-matched cohorts contain data from those individuals not shown in the immature and adult cohort.

4 Application of the set theory in demographic research

The set theory was used in life table research for the first time by Chi et al. (2022b) for a mathematical description, reasoning, deduction, and analysis of population demography.

A population or cohort is a set of n individuals and can be expressed as:

$$P = \{a_1, a_2, ..., a_n\} \tag{4.1}$$

where $a_1, a_2, ..., a_n$ represent n individuals. The total number of elements (i.e., the cardinality) of the set P is expressed as $|P|$ (Chartrand et al. 2008). It is clear that $|P| = n$. All fertile female individuals, i.e., individuals that reach the adult stage and produce offspring, form the set P_F

$$P_F = \{a_x : a_x \in P \text{ and } a_x \text{ is a fertile female}\} \tag{4.2}$$

Similarly, all fertile males compose the set P_M

$$P_M = \{a_x : a_x \in P \text{ and } a_x \text{ is a fertile male}\} \tag{4.3}$$

All nonreproducing individuals, i.e., individuals that died in the immature stages, infertile females, and infertile males, belong to the set P_N

$$P_N = \{a_x : a_x \in P \text{ and } a_x \text{ is an infertile individual}\} \tag{4.4}$$

It is clear that $P_F \subset P$, $P_M \subset P$, $P_N \subset P$, $|P_F| \leq |P|$, $|P_M| \leq |P|$, $|P_N| \leq |P|$ and $|P_F| + |P_M| + |P_N| = |P|$. The population set P (Equation 4.1) is the union set of P_F, P_M, and P_N,

$$P = P_F \bigcup P_M \bigcup P_N \tag{4.5}$$

The application of the set theory in life table research enables concrete and succinct formulation of equations in the following sections.

5 Bootstrap technique

The bootstrap technique was introduced four decades ago (Efron 1979). Currently, the bootstrap technique is being used in numerous research fields, e.g., information retrieval (IR) (Smucker et al. 2007), commercials on TV (Hesterberg 2008), economics (Horowitz 2019), insect demography (Huang & Chi 2012), and others. Bootstrap has been included in TWOSEX-MSChart program since 2012 (Huang & Chi 2012, Jha et al. 2012, Yu et al. 2013a, Yu et al. 2013b, Ebrahimi et al. 2013). Although Efron and Tibshirani (1993) mentioned that one disadvantage of using the bootstrap technique was the computational cost, this disadvantage has progressively diminished with the rapid advance of computer technology. In 1988, approximately 24 h were required to complete a jackknife analysis of a life table data using the computer program LIFETABL (Chi 1988) (previous version of TWOSEX-MSChart) and multiple weeks to complete a bootstrap resampling with $B = 1,000$ on an IBM PS-II with 80386 CPU. Bootstrap resampling today with $B = 100,000$ can be completed within a few minutes using the program TWOSEX-MSChart (Chi et al. 2022b, Chi 2023c).

Because the formulae for the intrinsic rate (Euler 1760, Lotka 1907) and the finite rate (Lewis 1942) are not closed-form equations and they are irrational numbers (except the theoretical values of $r = 0$ and $\lambda = 1$), numerical analysis (e.g., the bisection method, secant method, Newton-Raphson method) must be used to estimate these values (Chi 1982). When personal computers were still in their technological infancy, calculating the intrinsic rate and finite rate was exceedingly difficult; and, the estimation of uncertainty of population parameters was impossible. Meyer and his coworkers (Meyer et al. 1986) introduced the jackknife and bootstrap techniques, although use of the jackknife method for population parameters has since been invalidated by Huang and Chi (2013). Furthermore, substantially higher B values (e.g., 10,000 or 100,000) are now recommended when the bootstrap technique is used in the age-stage, two-sex life table analysis (Huang & Chi 2012, Akca et al. 2015). The bootstrap technique is now considered a fundamental tool in demographic research.

5.1 Combined application of set theory and bootstrap technique

When the bootstrap technique is applied to a life table analysis of an insect population, the definition of "population" differs from "statistical population". In general statistics, a population involves a single statistic, for example, wing length, body weight, blood pressure, etc. A biological population, on the other hand, is composed of individuals and each individual has many biological characteristics, e.g., sex, survived stages, longevity, first reproductive age, total fecundity, and many others. Therefore, when the bootstrap technique is applied to an arthropod population consisting of n individuals, every bootstrap sample is a set, P_b, composed of n individuals and all their characteristics randomly selected with replacement from P (Equation 4.1):

$$P_b = \{a_{x_1}, a_{x_2}, \cdots, a_{x_n}\} \text{ where } a_{x_i} \in P \text{ and } 1 \leq i \leq n. \tag{5.1}$$

Because the bootstrap technique is based on random sampling with replacement, an individual can be repeatedly sampled, i.e., $a_{x_i} = a_{x_k}$. All bootstrap samples of a cohort A using $B = 100,000$ form a set of all bootstrap samples, P_A

$$P_A = \{P_1, P_2, \cdots, P_B\} \tag{5.2}$$

The net reproductive rate (R_0) can be calculated for each bootstrap sample, P_b. Their total forms the set $R_{0,A}$

$$R_{0,A} = \{R_{0,1}, R_{0,2}, ..., R_{0,B}\} \tag{5.3}$$

However, when a bootstrap sample contains no fertile female individuals, no intrinsic rate (r) or finite rate (λ) can be calculated for that sample. Therefore, the set of all intrinsic rates (r_A) and the set of all finite rates (λ_A) may be smaller than $R_{0,A}$

$$r_A = \left\{ r_{A_1}, r_{A_2}, ..., r_{A_{B-d}} \right\} \tag{5.4}$$

$$\lambda_A = \left\{ \lambda_{A_1}, \lambda_{A_2}, ..., \lambda_{A_{B-d}} \right\} \tag{5.5}$$

where d is the number of infertile bootstrap samples. It is clear that $|\lambda_A| \leq |B_{0,A}|$ and $|r_A| \leq |B_{0,A}|$. Infertile samples are discussed in Section 5.4.

Because $\lambda = e^r$, it is evident that $r_{A_x} = \ln \lambda_{A_x}$ and $|\lambda_A| = |r_A|$. The percentile confidence interval of bootstrap estimates of R_0, λ, and r can be easily located from the sorted elements of $R_{0,A}$, λ_A, and r_A.

5.2 Larger sampling numbers generate more reliable confidence intervals

Because the bootstrap technique is based on computer simulation of random sampling with replacement, greater numbers of bootstrap resampling (B) will generate more precise estimates of standard errors and confidence intervals. Greater

numbers of B, however, entail longer computer time. Meyer et al. (1986) recommended $B = 500\sim1000$ based on a population of 10 *Daphnia pulex* Leydig (Cladocera: Daphniidae) individuals. Hesterberg (2008) pointed out that simulations for convergence of t intervals required 20,000 h in 1981. A larger B (10,000 or 100,000) is now considered necessary to obtain stable and precise statistics involving population parameters (Huang & Chi 2012, Akca et al. 2015). With the increased sophistication of computer techniques, the program TWOSEX-MSChart (Chi et al. 2022b, Chi 2023c) is able to complete a 100,000-bootstrap resampling within a few minutes for a population of 50 individuals. To demonstrate the effect of B, four bootstrap resamplings (i.e., $B = 1,000$, 10,000, 100,000, and 1,000,000), each with five replicates, were applied to the data from Taghizadeh & Chi (2022). When B equaled 1,000 or 10,000, the variability of the estimated R_0 was high at the 0.025, 0.5, and 0.975 percentiles (plots A1~A3 and B1~B3 of Fig. 5).

5.3 Using cumulative/additive bootstrap to achieve a greater bootstrap number

Because the bootstrap technique is based on computer simulation and each estimated parameter needs to be saved in computer memory, the number of bootstrap resamplings that a computer can carry out is limited by its RAM and CPU. The
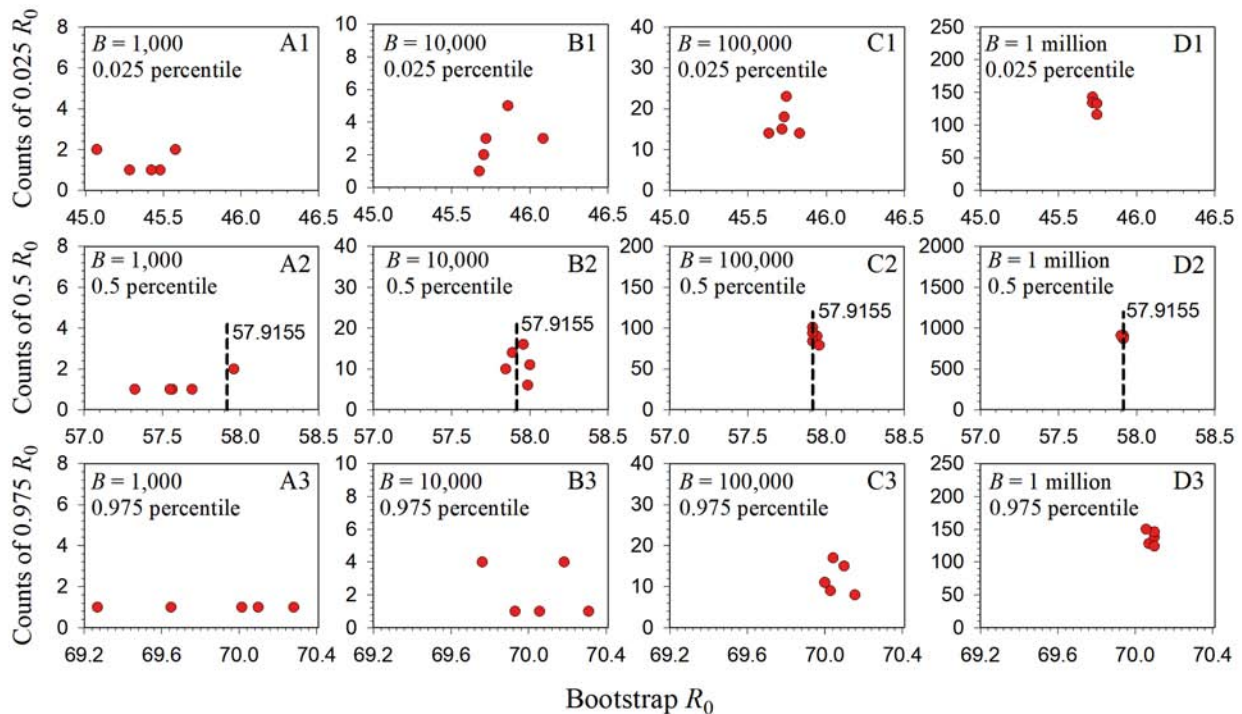
Fig. 5. Distribution and frequency (counts) of R_0 estimated by using $B = 1,000$, 10,000, 100,000 and 1,000,000 and five replicates when applied to Taghizadeh & Chi's data (2022). The vertical dashed line is the R_0 of the original cohort. For $B = 1,000$ or 10,000, greater variabilities were observed among five replicates of estimated R_0 at 0.025, 0.5, and 0.975 percentiles (plots A1~A3 and B1~B3), while smaller variabilities were observed when using 100,000 or 1,000,000 bootstrap resampling (plots C1~C3 and D1~D3).

current limit for the general version of TWOSEX-MSChart (Chi 2023c) is $B = 100{,}000$. A special version is available for $B = 1{,}000{,}000$, but the cohort size, longevity, and life stage parameters are limited.

Since all bootstrap samples are independent, a cumulative or additive bootstrap can be used to achieve a greater B value. For example, if 1,000,000 resampling is needed, the bootstrap procedure using $B = 100{,}000$ can be repeated 10 times and then all results are pooled in a figure or in a comparison using a paired bootstrap test. "Cumulative bootstrap" and "additive bootstrap" with different definitions have been used for different purposes (Schumacher et al. 1997, Van Ginkel & Kiers 2011, Jelassi & Delhoumi 2017). Herein, we define cumulative/additive bootstrap as simply combining bootstrap results to existing bootstraps using repetitive bootstrap procedures. By using the "append" computer function, bootstrap samples can be coupled with previous sampling results. In so doing, more precise estimates of standard errors and confidence intervals of a given population parameter, as well as paired bootstrap test can be obtained.

5.4 Fertile and infertile bootstrap samples

In the application of bootstrap technique in life table analysis, it is essential to consider differences in mating strategies (Chi et al. 2022b). If two-sex mating is necessary for successful reproduction, bootstrap cohorts consisting entirely of females and N-type individuals but with no fertile males are infertile; they are the elements of the set $P_{b,FN}$

$$P_{b,FN} = \left\{ \left\{ a_{x_1}, \cdots, a_{x_n} \right\} : a_{x_i} \in P_F \text{ or } a_{x_i} \in P_N \right\} \tag{5.6}$$

Bootstrap cohorts consisting of males and N-type individuals but with no fertile females are also infertile, and belong to the set $P_{b,MN}$

$$P_{b,MN} = \left\{ \left\{ a_{x_1}, \cdots, a_{x_n} \right\} : a_{x_i} \in P_M \text{ or } a_{x_i} \in P_N \right\} \tag{5.7}$$

Similarly, cohorts consisting of only N-type individuals are infertile and form the set $P_{b,N}$

$$P_{b,N} = \left\{ \left\{ a_{x_1}, \cdots, a_{x_n} \right\} : a_{x_i} \in P_N \right\} \tag{5.8}$$

The set of all infertile bootstrap samples, P_I, is the union set of $P_{b,FN}$, $P_{b,MN}$, and $P_{b,N}$

$$P_I = P_{b,FN} \bigcup P_{b,MN} \bigcup P_{b,N} \tag{5.9}$$

The difference of the two sets A and B is defined as

$$A - B = \left\{ x : x \in A \text{ and } x \notin B \right\}. \tag{5.10}$$

The set of all fertile samples, P_E, is the difference between P_A (Equation 5.2) and P_I

$$P_E = P_A - P_I \tag{5.11}$$

In parthenogenetic populations, bootstrap samples with one or more reproductive female are fertile samples and form the set P_E, while cohorts composed of only infertile individuals are infertile samples and form the set P_I and will go to extinction.

$$P_I = P_{b,N} = \left\{ \left\{ a_{x_1}, \cdots, a_{x_n} \right\} : a_{x_i} \in P_N \right\} \tag{5.12}$$

Equation 5.11 can also be used to calculate the set of fertile bootstrap samples in parthenogenetic populations.

By using the Venn diagram, the set of fertile and infertile bootstrap samples of bisexual and parthenogenetic populations can be accurately represented in Fig. 6. The circle B_M is the set of bootstrap samples containing one or more fertile males, B_F is the set of bootstrap samples containing one or more fertile females, and B_N is the set containing one or more N-type individuals.

In bisexual populations (Fig. 6A), the intersection of B_M and B_F is the set of fertile bootstrap samples (B_E), i.e., $B_F \cap B_M$; while the intersection of B_M, B_F, and B_N, e.g., $B_M \cap B_F \cap B_N$ is the set of fertile bootstrap samples containing females, males, and N-type individuals; thus, $\left(B_M \cap B_F \cap B_N \right) \subset B_E$. It is clear that $P_A = B_F \bigcup B_M \bigcup B_N$. Since $\left(B_M \cap B_F \cap B_N \right) \subset \left(B_M \cap B_F \right) = B_E$, all bootstrap samples belonging to $B_M \cap B_F$ can be used to calculate the probability of fertile samples.

Therefore, the set of all infertile samples (B_I) is

$$B_I = B_N - B_F - B_M = (B_F \cup B_M \cup B_N) - (B_F \cup B_M). \tag{5.13}$$

In the parthenogenetic populations, B_F is the set of bootstrap samples containing one or more fertile females, and it is the set of fertile bootstrap samples. The intersection of B_F and B_N, i.e., $B_N \cap B_F$, is the set of fertile bootstrap samples containing both females and N-type individuals. The set of infertile bootstrap samples is

$$B_I = B_N - B_F = \left(B_F \bigcup B_N \right) - B_F. \tag{5.14}$$
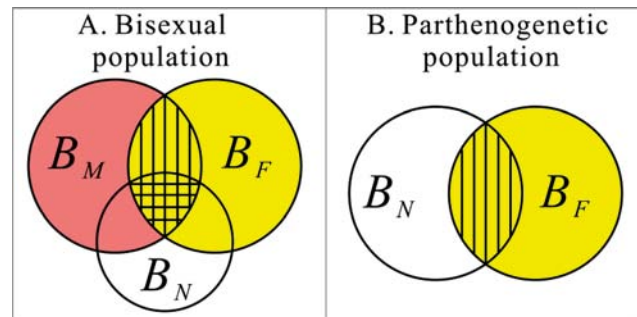

Fig. 6. Venn diagrams of fertile and infertile bootstrap samples of bisexual populations **(A)** and parthenogenetic populations **(B)**. The circle B_M is the set of bootstrap samples containing one or more fertile males, the circle B_F is the set of bootstrap samples containing one or more fertile females, and the circle B_N is the set containing one or more N-type individuals.

Because the bootstrap technique is based on random sampling with replacement and B is limited, in general the sets B_M, B_F, and B_N are only a small portion of the real sample space and the elements of B_M, B_F, and B_N vary with each bootstrap resampling. Therefore, the union of B_M, B_F, and B_N, i.e., $B_M \bigcup B_F \bigcup B_N$, is not the actual sample space. The true sample space will be discussed in Section 6. Chartrand et al. (2008) discusses a more detailed introduction to set theory.

5.5   Why is it necessary to consider infertile bootstrap samples?

The observed probabilities of fertile and infertile bootstrap samples can be calculated from the bootstrap results. If the proportion of infertile individuals is low (Fig. 7A), the probability of fertile and infertile individuals in bootstrap samples will be similar. However, if the proportion of infertile individuals is high but bootstrap sampling is limited to fertile samples, there will be a biased selection favoring fertile individuals that will result in biased estimates (Fig. 7B).

Therefore, infertile bootstrap samples must also be included to accurately estimate population parameters when using bootstrap technique. Since all bootstrap samples are randomly selected, the probability of an observed bootstrap sample varies with each simulation. To calculate the theoretical probability, it is necessary to use the multinomial theorem, which is discussed in Section 6.

6   Multinomial theorem

There is, inevitably, theory behind technique. Some theories are developed prior to the technology being available, e.g., the atomic theory was well-known prior to the development of a nuclear bomb. On the other hand, technologies have been developed before the theory, e.g., the wheel was invented well before we understood geometry and π. The mathematical basis of bootstrap technique is the multinomial theorem.

6.1   Using the multinomial theorem to decode the bootstrap technique

Zhao et al. (2021), Ding et al. (2021), and Taghizadeh and Chi (2022) applied the multinomial theorem (Equation 6.1) in their demographic research:

$$(a_1 + a_2 + \cdots + a_n)^n = \sum_{\substack{(n_1, \cdots, n_n): \\ n_1 + \cdots + n_n = n}} \binom{n}{n_1, n_2, \cdots, n_n} a_1^{n_1} a_2^{n_2} \cdots a_n^{n_n} \tag{6.1}$$

where $\binom{n}{n_1, n_2, \cdots, n_n}$ is the multinomial coefficient and it is calculated as Equation 6.2:

$$\binom{n}{n_1, n_2, \cdots, n_n} = \frac{n!}{n_1! n_2! \cdots n_n!} \tag{6.2}$$

where $n_i \geq 0$ and $n_1 + n_2 + \cdots + n_n = n$. Equation 6.2 represents the number of possible sampling ways (in mathematical terms, "permutation") needed to get the combination of $a_1^{n_1} a_2^{n_2} \cdots a_n^{n_n}$ using bootstrap technique. Although the bootstrap samples of a cohort form a set of all bootstrap samples P_A (Equation 5.2), it is generally impossible to detect the true sample space using bootstrap technique due to the limited B. The total number of all possible bootstrap resampling is n^n, i.e., all possible permutations of selecting n individuals from a cohort of n individuals with replacement. Therefore, all items of the expansion of Equation 6.1 equals the exact and true sample space S,
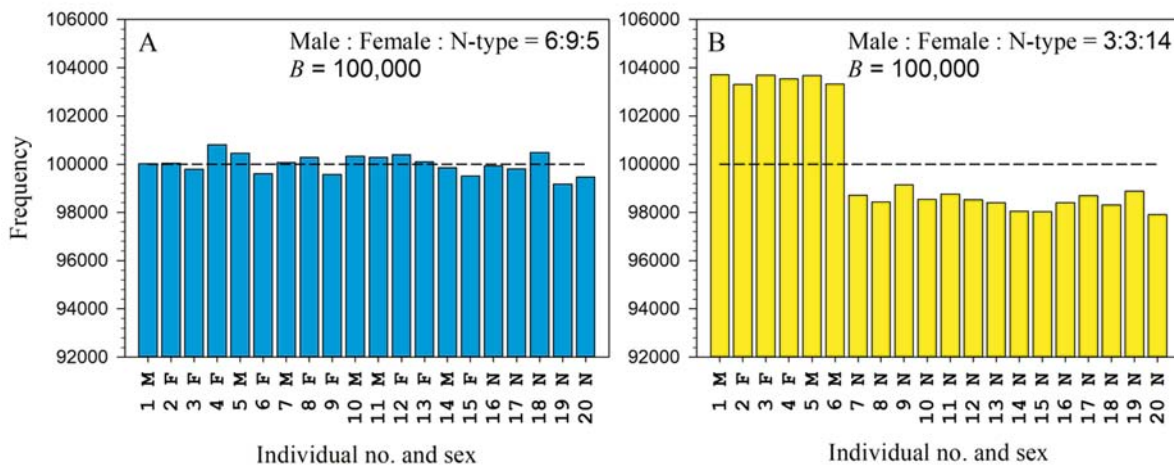

Fig. 7. Frequency of individuals selected in bootstrap samples. **A.** Cohort with 25% N-type individuals. **B.** Cohort with 70% N-type individuals.

$$S = \left\{ \left\{ a^{n_1}, \cdots, a^{n_n} \right\} : 0 \leq n_i \leq n \text{ and } n_1 + n_2 + \cdots + n_n = n \right\} \tag{6.3}$$

This sample space generally cannot be detected by using the bootstrap technique on contemporary personal computers when $n > 15$. It is obvious that $P_A = B_F \bigcup B_M \bigcup B_N$ (Equation 5.2) is a subset of S, i.e., $P_A \subset S$. Therefore, it is critical that the multinomial theorem is used to determine the unbiased and true sample space in bootstrap technique. The sum of all multinomial coefficients (i.e., S_M) of Equation 6.1 gives all possible sampling procedures (permutation) and

$$S_M = \sum_{\substack{(n_1 \cdots, n_n): \\ n_1 + \cdots + n_n = n}} \binom{n}{n_1, n_2, \cdots, n_n} = n^n \tag{6.4}$$

For a cohort with n individuals, the total number of items (L) of $a_1^{n_1} a_2^{n_2} \cdots a_n^{n_n}$ (i.e., different individual compositions or bootstrap life tables on the right-hand side of Equation 6.1) is

$$L = \binom{2n-1}{n} = \binom{2n-1}{n-1} = C(2n-1, n) = C(2n-1, n-1) \tag{6.5}$$

where C stands for combination. The probability of a specific bootstrap sample $a_1^{n_1} a_2^{n_2} \cdots a_n^{n_n}$ can then be calculated as

$$P_r \left(a_1^{n_1} a_2^{n_2} \cdots a_n^{n_n} \right) = \frac{\binom{n}{n_1, n_2, \cdots, n_n}}{n^n} = \frac{\binom{n}{n_1, n_2, \cdots, n_n}}{S_M} \tag{6.6}$$

Efron & Tibshirani (1993) presented this probability as Equation 6.7 (Equation 6.16 in Efron & Tibshirani 1993):

$$\binom{n}{j_1, j_2, \cdots, j_n} \prod_{i=1}^{n} \left(\frac{1}{n} \right)^{j_i} \tag{6.7}$$

where $j_1 + j_2 + \cdots + j_n = n$. For computer programming, Equation 6.6 is an easier option without the Π notation (i.e., the repeated multiplication).

6.2 Probability of bootstrap samples being the same as the original cohort

If a bootstrap sample is composed of the same individuals as the original cohort, it will produce the same population parameters, even though the sampling orders of individuals will be different. The number of sampling ways of obtaining such a bootstrap life table, i.e., every individual appears exactly one time, can be calculated as

$$\binom{n}{1, 1, \cdots, 1} = \frac{n!}{1! 1! \cdots 1!} = n! \tag{6.8}$$

For any $n_x > 1$, it is clear that

$$\binom{n}{n_1, n_2, \cdots, n_n} = \frac{n!}{n_1! n_2! \cdots n_n!} < \binom{n}{1, 1, \cdots, 1} = \frac{n!}{1! 1! \cdots 1!} = n! \tag{6.9}$$

Therefore, Equation 6.8 is the greatest multinomial coefficient of Equation 6.1 and the probability of taking a bootstrap sample which is the same as the original cohort is higher than other bootstrap samples and can be calculated as

$$P_r \left(a_1^1 a_2^1 \cdots a_n^1 \right) = \binom{n}{1, 1, \cdots, 1} \Big/ n^n = \frac{n!}{n^n} \tag{6.10}$$

For a small cohort with five individuals, the total possible combinations of bootstrap are $5^5 = 3125$. The number of combinations that are the same as the original cohort is $5! = 120$. The probability of a bootstrap life table being the same as the original one is $120/3125 = 0.0384$. If $B = 100,000$, there will be approximately 3,840 original life tables among the 100,000 bootstrap life tables. When $n = 15$, $P_r \left(a_1^1 a_2^1 \cdots a_n^1 \right) = 2.986 \times 10^{-6}$; using $B = 500,000$, the expected number of life tables with the same R_0 of the original cohort is very close to the observed one (Figure 9 in Zhao et al. 2021). However, for a cohort with 71 individuals, all possible samplings are 71^{71} (i.e., 2.75×10^{121}); using $B = 100,000$, it would be unfeasible in this case to attempt to generate all possible combinations by using the multinomial theorem (Equation 6.1), because $100,000 = 10^5 \ll 71^{71} = 2.75 \times 10^{121}$. Ross (2006) introduced additional details covering probability.

6.3 Observed number of different F, R_0, r, and λ using bootstrap technique

The total number of different life tables (different combinations of individuals) in a cohort with a population of 71 individuals (*c.f.* Taghizadeh & Chi 2022) was determined to be $L = 1.86 \times 10^{41}$ (using Equation 6.5). One million life tables were obtained when the bootstrap technique was used in this paper with $B = 1,000,000$. There were 785,799 different finite rates and 4,521 different R_0 values (there were 4,521 data points in Fig. 8A). It is obvious that $4,521 \ll 785,799 \ll 1.86 \times 10^{41}$. The 4,521 different R_0 values, however, was higher than the 2,795 R_0 values they observed when they used $B = 100,000$ (there were 2,795 data points in their Fig. 5A (Taghizadeh & Chi 2022)). Among the one million life tables, not a single one was the same as the original cohort. This fact is evident when Equation 6.10 is used and generates the probability that a bootstrap life table being identical to the original is $3.09 \times 10^{-30} \approx 0$.

The sum of the multinomial coefficients of 1,000,000 life tables was 1.2281×10^{100}., i.e., $S_{M, Observed} = 1.2281 \times 10^{100}$. Some R_0 values appeared more frequently than others among the 4,521 different R_0 values. There were 869 observed life tables with the same R_0 as the original cohort ($R_{0, original} = 57.91549$), i.e., the count of $R_{0, original}$ in Fig. 8A and 8C was 869. The observed 869 samples belong to 841 different combinations (different life tables). The sum of multinomial coefficients of these 841 life tables was 1.13133×10^{97}, i.e., $S_{M, Observed} = 1.13133 \times 10^{97}$. The probability of 1.13133×10^{97} among 1.2281×10^{100} was 0.0009212. The expected counts were then $0.0009212 \times 1000000 = 921$. The observed 869 counts among all 1,000,000 counts was close to the the-
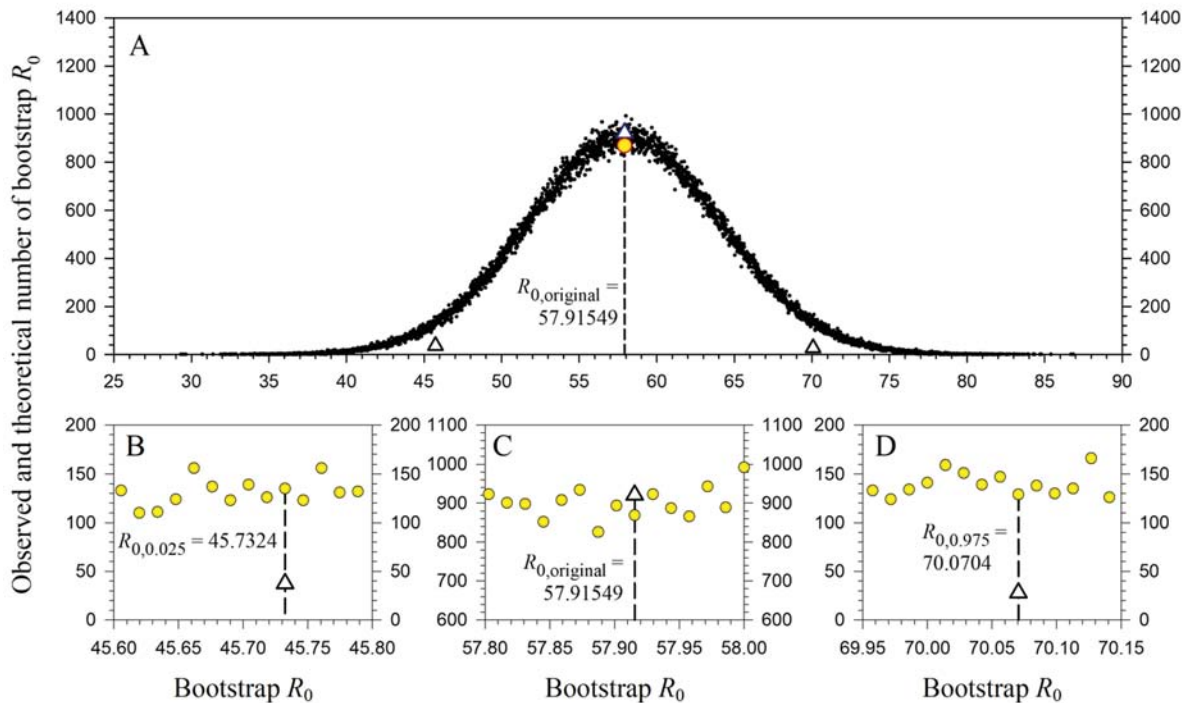
Fig. 8. Distribution of bootstrap R_0 using $B = 1,000,000$ **(A)**. The dots and circles are the observed values. The triangles are the expected (theoretical) values calculated by using the multinomial coefficients. The 0.025, original, and 0.975 regions are enlarged in subplots **B**, **C**, and **D**, respectively.

oretical 921. Because it is currently unfeasible to determine the exact number of different R_0 values that may be present in 86×10^{41} life tables, it is, therefore, not possible to calculate an accurate probability for the presence of a specific R_0 using Equation 6.6. Additional information regarding the theoretical number (counts) of different R_0 values obtainable through use of the multinomial theorem is included in the following section.

The number of different λ and r values obtained by using $B = 1,000,000$ is 785,799 (there are 785,799 points in Fig. 9A). The result obtained by using the bootstrap technique is only a minute percentage of the theoretical values.

6.4 The theoretical number of R_0 observed in bootstrap samples

The number of observed bootstrap samples generated by using the bootstrap technique is dependent on n and B; e.g., if $n = 6$, the theoretical number of samplings is $S_M = 6^6 = 46656$ (Equation 6.4) and the theoretical number of different life tables is $L = 462$. Therefore, if $n = 6$ and $B = 100,000$ (> 46656), it is theoretically feasible to obtain all possible bootstrap samples 46656 and 462 different life tables. Because a large cohort (e.g., $n = 30$) is usually necessary for a life table study, it is impossible to obtain all possible bootstrap life tables with $B = 100,000$ or $1,000,000$ ($S_M = 30^{30}$, $L = 5.9 \times 10^{16}$).

In Fig. 8 ($n = 71$ and $B = 1$ million), the probability of every observed bootstrap sample among 1,000,000 is $1/B = 0.000001$. However, the theoretical probability of every bootstrap sample is infinitesimal (i.e., $1/71^{71}=3.64\times10^{-132}$), while the L value for 71 individuals is 1.86×10^{41}. Therefore, when $B = 1,000,000$ only a tiny fraction of all possible life tables can be observed. Although the numbers of observed F, R_0, r, and λ will always vary depending on the simulations, the theoretical probability and expected number of any bootstrap sample can be calculated based on its multinomial coefficient and the value of B (the Button A5 in TWOSEX-MSChart). Different combinations of individuals, however, can have the same mean fecundity (F). Chi (1988) proved mathematically that the relationship between the net reproductive rate (R_0) and mean fecundity (F) is $R_0 = F \times N_f/N$, where N_f is the number of female adults emerged from the cohort size N. If two bootstrap samples have the same N_f and F values, their corresponding values of R_0 values will be the same. However, if two have a different N_f but the same F, they will have a different R_0. On the other hand, if two bootstrap cohorts have different F and N_f, they may have the same or different R_0. Moreover, two cohorts having the same R_0 and F values may produce different r and λ when eggs that are laid at different ages make different contribution to r and λ (Lewontin 1965). Therefore, when $n > 2$ it is easy to prove that
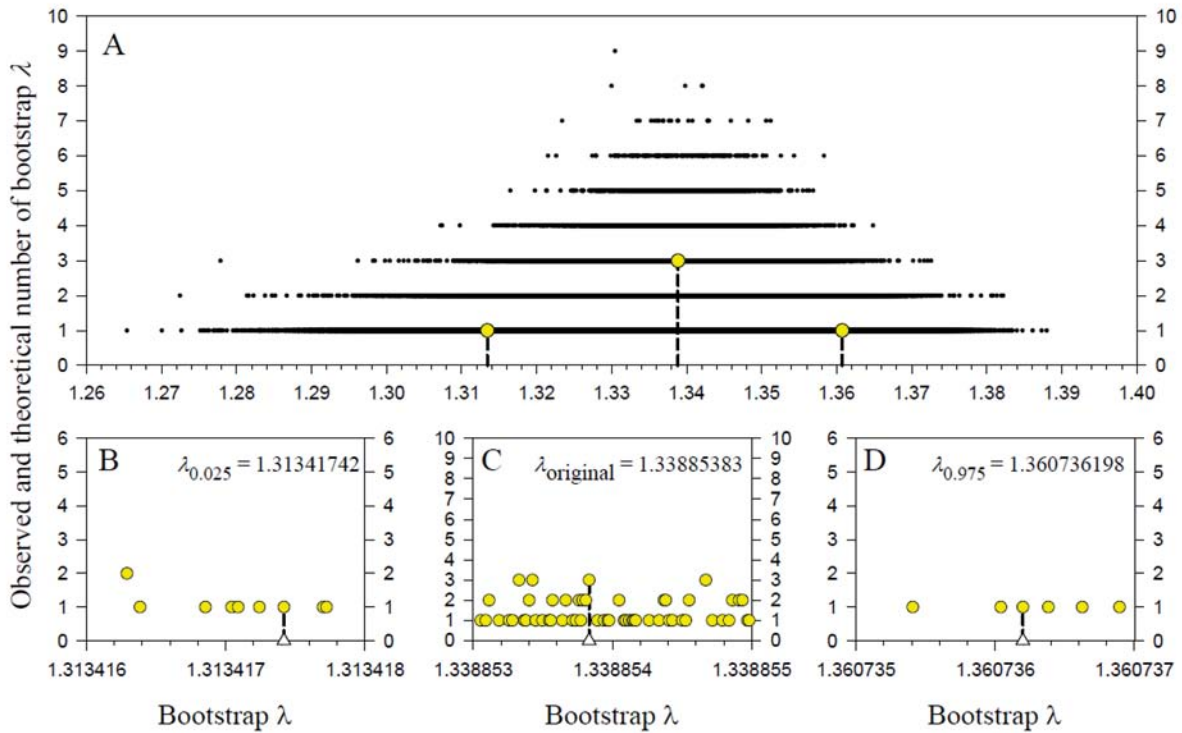
Fig. 9. Distribution of bootstrap λ using B = 1,000,000. The dots and circles are the observed values. The triangles (seemly on the x-axes) are the theoretical values.

$$N_{r,Th} = N_{\lambda,Th} \geq N_{R_0,Th} \tag{6.11}$$

When $n \geq 6$ and $B = 1,000,000$, it is obvious that

$$L \geq N_{r,Ob} = N_{\lambda,Ob} \geq N_{R_0,Ob} \tag{6.12}$$

where $N_{r,Th}$, $N_{\lambda,Th}$, and $N_{R_0,Th}$ represents the theoretical numbers of r, λ, and R_0, respectively, when calculated by using the multinomial theorem; while $N_{r,Ob}$, $N_{\lambda,Ob}$, and $N_{R_0,Ob}$ represents the observed number of r, λ, and R_0, respectively, when using the bootstrap technique. Based on the individual compositions of observed bootstrap samples, their theoretical values, $N_{r,Th}$, $N_{\lambda,Th}$, and $N_{R_0,Th}$ can be calculated using the multinomial theorem (Equations 6.1 and 6.2). Their theoretical probabilities can be calculated using Equation 6.6.

As seen in Fig. 8 ($n = 71$ and $B = 1$ million), the total number of observed $R_0 = 57.91549$ is 869, which is close to the theoretical counts of 921 (Fig. 8A and 8C). However, the number of observed R_0 of the 0.025 and 0.975 percentiles (135 and 128, respectively), are clearly higher than their respective theoretical values of 38 and 28 (Fig. 8B and 8D). In most cases, the theoretical counts of 0.025 and 0.975 R_0 will be lower than the observed ones. This is analogous to the lottery. In general, the number of theoretically possible combinations in a lottery (n_T) is huge compared to the actual

number of ways of winning the grand price (n). The probability (P_T) of winning the grand price is extremely low, i.e., $P_T = n/n_T \rightarrow 0$. Occasionally, a lucky individual will win the grand prize. If the number of lottery tickets sold (n_s) is used as the denominator to calculate the observed probability of winning, P_o ($P_o = 1/n_s$), then P_o is an illusional figure which is much greater than the theoretical one, i.e., $P_o \gg P_T$.

6.5 Theoretical probability of fertile and infertile bootstrap samples

All possible combinations of bootstrap samples, including fertile and infertile bootstrap samples, can be correctly calculated by using the multinomial theorem. Since the result of infertile bootstrap samples is $R_0 = 0$, it is impossible to calculate the intrinsic and finite rates for these samples. Because female age-specific life tables overlook the male population, they are incapable of detecting these ineffective bootstrap samples of two-sex populations. This major drawback of using female age-specific life tables was discussed by Huang and Chi (2012) and Huang et al. (2018).

6.5.1 Probability of fertile and infertile bootstrap samples in two-sex populations

According to Chi et al. (2022b), the probability of obtaining infertile bootstrap samples can be calculated as:

$$P_{r,I} = P_{r,FN} + P_{r,MN} - P_{r,N} \tag{6.13}$$

where $P_{r,FN}$ is the probability of obtaining samples that contain only females and those individuals died during the preadult stages, and it is calculated as:

$$P_{r,FN} = \frac{\left(n_f + n_N\right)^n}{n^n} \tag{6.14}$$

where n_f is the number of fertile females and n_N is the number of N-type individuals. $P_{r,MN}$ is the probability of obtaining samples that contain only males and those individuals died during the preadult stages, and it is calculated as

$$P_{r,MN} = \frac{\left(n_m + n_N\right)^n}{n^n} \tag{6.15}$$

where n_m is the number of fertile males. $P_{r,N}$ is the probability of obtaining samples that contain only those individuals died during the preadult stage, and it is calculated as

$$P_{r,N} = \frac{\left(n_N\right)^n}{n^n} \tag{6.16}$$

The probability of fertile bootstrap samples can be calculated as:

$$P_{r,E} = \left(1 - P_{r,FN} - P_{r,MN} + P_{r,N}\right) = \left(1 - P_{r,I}\right) \tag{6.17}$$

6.5.2   Probability of fertile and infertile bootstrap samples of parthenogenetic populations

When dealing with parthenogenetic populations, the probability of obtaining infertile and fertile bootstrap samples can be calculated using Equations 6.18 and 6.19:

$$P_{r,I} = P_{r,N} \tag{6.18}$$

$$P_{r,E} = \left(1 - P_{r,I}\right) \tag{6.19}$$

7   Assessing differences between treatments

7.1   Paired bootstrap test

Comparing the results of different treatments is a critical component of scientific research. In the two-sex life table data analysis, the paired bootstrap test based on the distribution of differences of paired bootstrap results of two treatments is used to assess the differences between treatments in a pairwise fashion (Smucker et al. 2007, Figuera et al. 2009, Wei et al. 2020). When the paired bootstrap test is used to assess the differences between hypothetical treatments A and C, the unsorted (or random) bootstrap results of A and C are used to calculate the differences. Because the bootstrap results are unsorted, the observed differences can reveal the possible random differences between treatments. All paired differences, i.e., $R_{0,A_x} - R_{0,C_x}$ form the set $R_{0,A-C}$

$$R_{0,A-C} = \left\{R_{0,A_1} - R_{0,C_1}, R_{0,A_2} - R_{0,C_2}, ..., R_{0,A_B} - R_{0,C_B}\right\} \text{ and}$$
$$\left|R_{0,A-C}\right| = B \tag{7.1}$$

The sorted differences of all elements of Equation 7.1 can be used to find the percentile confidence intervals of differences between treatments (normally the 0.025th and 0.975th percentiles) (Wei et al. 2020). If the percentile confidence intervals include zero, there is no significant difference between treatments. It is clear that the same bootstrap number (B) must be used for the two treatments (A and C) when conducting the paired bootstrap test.

Data of Taghizadeh and Chi (2022) are illustrated in Fig. 10 to demonstrate the paired bootstrap test between the R_0 values of their 150 and 225 g nitrogen treatments.

7.2   Cartesian paired test based on Cartesian products of bootstrap samples

Chi et al. (2022b) introduced the application of the Cartesian products to calculate all possible differences between bootstrap samples of two treatments (A and C). The Cartesian product of two sets of the net reproductive rates of bootstrap samples, i.e., $R_{0,A}$ with B bootstrap resampling and $R_{0,C}$ with D bootstrap resampling, is the set whose first element belongs to $R_{0,A}$ and whose second element belongs to $R_{0,C}$ (Chartrand et al. 2008, Chi et al. 2022b).

$$R_{0,A} \times R_{0,C} = \left\{\left(R_{0,A_x}, R_{0,C_y}\right) : R_{0,A_x} \in R_A, x \leq B \text{ and}\right.$$
$$\left. R_{0,C_y} \in R_C, y \leq D\right\} \tag{7.2}$$

The differences of all pairs of the Cartesian products $R_{0,A} \times R_{0,C}$ is a set $\Delta_{R_0,A-C}$ that will definitely include all possible differences of the bootstrap results of $R_{0,A}$ and $R_{0,C}$.

$$\Delta_{R_{0,A-C}} = \left\{R_{0,A_1} - R_{0,C_1}, R_{0,A_1} - R_{0,C_2}, R_{0,A_1} - R_{0,C_3}, \cdots, R_{0,A_1} - R_{0,C_D},\right.$$
$$R_{0,A_2} - R_{0,C_1}, R_{0,A_2} - R_{0,C_2}, R_{0,A_2} - R_{0,C_3}, \cdots, R_{0,A_2} - R_{0,C_D}, \cdots,$$
$$\left. R_{0,A_B} - R_{0,C_1}, R_{0,A_B} - R_{0,C_2}, R_{0,A_B} - R_{0,C_3}, \cdots, R_{0,A_B} - R_{0,C_D}\right\} \tag{7.3}$$

and $\left|\Delta_{R_0,A-C}\right| = \left|R_{0,A}\right| \times \left|R_{0,C}\right| = B \times D$. The data used in Fig. 10 is also used in the Cartesian paired test (CPT) as seen in Fig. 11.

There are two main advantages of the Cartesian paired test over the general paired bootstrap test: (1) The comparison is complete, i.e., it includes all possible differences in the bootstrap results of two treatments. (2) The number of bootstrap samples of two treatments can be different (i.e., $B \neq D$). The distribution of differences in the Cartesian paired test (Fig. 11B) is obviously better than that shown using the general paired bootstrap test (PBT) (Fig. 10B), and was closer to a normal distribution. Although there was no significant difference between treatments in this particular example
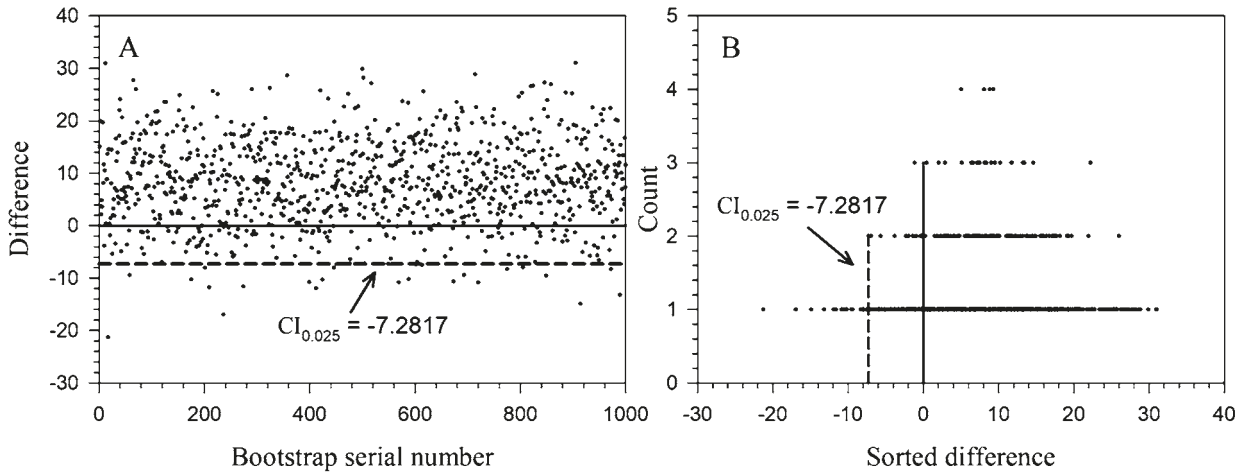
Fig. 10. A. Unsorted differences of the R_0 values of 1,000 bootstrap resamples of two N treatments (150 N and 225 N). **B.** Sorted differences of R_0 values of 1,000 bootstrap resamples of 150 N and 225 N treatments (Data from Taghizadeh & Chi 2022).
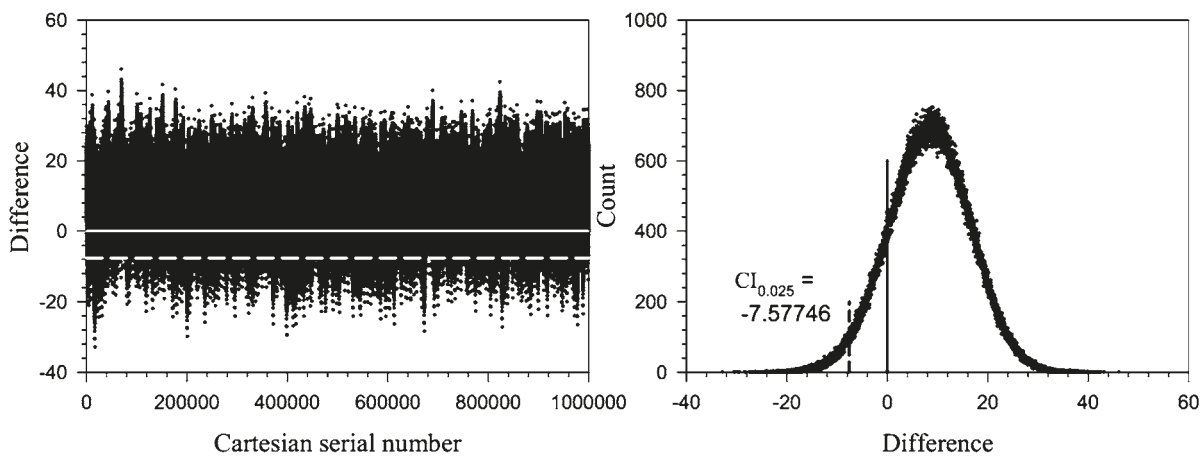

Fig. 11. A. Unsorted 1,000,000 Cartesian differences in R_0 values between two N treatments (150 N and 225 N). **B.** Sorted 1,000,000 Cartesian differences of R_0 (Data from Taghizadeh & Chi 2022). The solid lines are zero and the dashed lines are the 0.025 percentile of differences. (Because of the large amount of data contained in Fig. 11, it is shown separately from Fig. 10.)

(Figs. 10 and 11), CPT may be able to detect difference in other situations that may be missed when PBT is used.

7.3   Cartesian paired test based on the multinomial theorem

The Cartesian paired test discussed in Section 7.2 is based on the bootstrap samples of treatments A and C, and covers all possible bootstrap differences of Cartesian pair of $R_{0,A}$ and $R_{0,C}$. However, because bootstrap is based on random sampling with replacement, the results of Cartesian paired test vary with simulation. The bootstrap results generally cannot include all possible samples of the multinomial theorem (Equation 6.5). However, if all items of the multinomial

theorem (Equation 6.1) of the two cohorts A and C are used in the Cartesian products, a complete or true Cartesian products and Cartesian paired test can be achieved. If there are n individuals $\left(a_1, a_2, \cdots, a_n\right)$ in cohort A, the total number of sampling possibilities (permutations) from A is n^n and the total number of different bootstrap life tables is $L_A = C(2n-1, n)$, i.e., the number of items at the right-hand side of Equation 6.1. Assuming there are 4 individuals in cohort A, the expansion of the multinomial theorem generates the set Q_A. This set contains $S_M = 4^4 = 256$ elements (theoretical sampling possibilities or cohorts) and the number of different life tables in this set will be $L_A = C(2 \times 4 - 1, 4) = 35$. The net reproductive rate of all 256 cohorts is the set

$$R_{0,A} = \left\{ R_{0,A_1}, R_{0,A_2}, ..., R_{0,A_{256}} \right\} \qquad (7.4)$$

If there are m individuals $\left(c_1, c_2, \cdots, c_m\right)$ in cohort C, the total number of sampling possibilities from C is m^m and there are $L_C = C(2m-1,m)$ items (i.e., bootstrap life tables). Assuming there are 5 individuals in cohort C, the set Q_C contains 3125 elements (possible theoretical samplings or cohorts) and the number of different life tables in Q_C is $L_C = C(2m-1,m) = C(2\times5-1,5) = 126$. The net reproductive rate of these 3125 cohorts is the set

$$R_{0,C} = \left\{ R_{0,C_1}, R_{0,C_2}, ..., R_{C_{3125}} \right\} \qquad (7.5)$$

The Cartesian paired test based on the multinomial theorem is

$$\Delta_{R_{0,A-C}} = \left\{ R_{0,A_1} - R_{0,C_1}, R_{0,A_1} - R_{0,C_2}, R_{0,A_1} - R_{0,C_3}, ..., R_{0,A_1} - R_{0,C_{3125}}, \right.$$
$$R_{0,A_2} - R_{0,C_1}, R_{0,A_2} - R_{0,C_2}, R_{0,A_2} - R_{0,C_3}, ..., R_{0,A_2} - R_{0,C_{3125}}, \cdots,$$
$$\left. R_{0,A_{256}} - R_{0,C_1}, R_{0,A_{256}} - R_{0,C_2}, R_{0,A_{256}} - R_{0,C_3}, ..., R_{0,A_{256}} - R_{0,C_{3125}} \right\} \qquad (7.6)$$

In this example, it is evident that $|\Delta_{0,A-C}| = 256\times3125 = 800000$. These 800,000 differences are the exact number of differences using the Cartesian paired test based on the multinomial theorem. The sorted $\Delta_{0,A-C}$ gives the exact confidence intervals. Although applying the Cartesian paired test is currently unfeasible due to the limited RAM and CPU available with current personal computers, we are anticipating being able to do so in the near future.

8   Advanced application of the life table: integrating life tables, predation/parasitism, and computer simulation

Chi (1990) discussed the importance of using computer simulation for calculating the optimal timing of various procedures in planning pest management programs based on the stage structure of the pest population, while Rapp (1992) noted that computer simulation was a relatively new method for use in scientific research in addition to the abstract reasoning and experimental reasoning. Computer simulation enables scientists to conduct increasingly complicated systems research. Gharekhani et al. (2020) used the age-stage, two-sex life table to evaluate the tri-trophic interactions among nitrogen fertilized tomato cultivars, the tomato fruit worm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) and the ectoparasitoid, *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae).

8.1   Computer simulation considering the stage-specific characteristics

Ding et al. (2021) integrated using the age-stage, two-sex life table, stage-specific predation rate, and computer simulation

to evaluate the biological control efficacy of *Orius strigicollis* (Poppius) (Hemiptera: Anthocoridae). By using the life table and stage-specific parasitism rate, Wei et al. (2022) contrasted the fitness of the parasitoid *A. japonicus* reared on *A. pernyi* and *C. japonica*. They demonstrated that *A. japonicus* had a higher net reproductive rate (R_0) when reared on eggs of *A. pernyi* and the emerged adult parasitoids had a high net parasitism rate (P_0) when used against *C. japonica*. They concluded that parasitoids reared on eggs of the Chinese oak silkworm have a high biological control potential against the Japanese giant silkworm. Asgari et al. (2022) linked their studies on the life table and age-stage-specific predation rate of the predatory mite, *Blattisocius mali* Oudemans (Mesostigmata: Blattisociidae) against the stored product mites, *Tyrophagus putrescentiae* (Schrank) (Sarcoptiformes: Acaridae). Islam et al. (2022a) linked their life table with predation rate to assess the effects of temperatures on the population growth and predation potential of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) reared on *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae). Their data showed a higher net predation rate (C_0) at lower temperatures (15 and 20°C), while the finite predation rates (ω) increased at higher temperatures (25 and 30°C). Moreover, their computer simulation predicted a higher predation potential at higher temperatures. Islam et al. (2022b) studied the predation rate of *H. axyridis* on the eggs of *Spodoptera litura* (F.) (Lepidoptera: Noctuidae). They reported there was no significant difference in the net predation rate (C_0) between 15 and 30°C, however, the finite predation rate (ω) at 30°C was significantly higher than that at 15°C.

8.2   Predator-prey relationships based on life tables

Studying the interactions between predators or parasitoids and their prey or hosts is an economically important aspect of ecology and biological control. Simple models such as the Lotka-Volterra model are not applicable to biocontrol programs, because they ignore age and stage structure. Holling (1959a, b) developed the disc equation using "sandpaper discs" and "blind-folded subject" in his experiment. Since then, Holling's functional responses have been studied extensively. Nowadays, Holling's experiment can be easily replicated using computer simulation. Holling noted in his 1959 publication (1959a) that "observations in the field and laboratory showed that only one of the life stages was attacked by the small-mammal predator, and that the remaining stages were inaccessible and/or unpalatable and hence completely escaped attack". His statement demonstrated that the stage structure of a prey population can be an important issue. The age-stage, two-sex life table is an important tool in studying similar predator-prey relationships. Because most research focused on functional responses only chronicles the predation rate within a short time period (e.g., 24 h), this small sample of behavior is likely insufficient for obtaining

a complete understanding of the predator-prey relationship. Since the predation/vulnerability will often vary with stage and age, it is necessary to characterize the predator-prey relationship based on their life tables. Because the predator-prey relationship based on the age-stage, two-sex life table covers the entire life span of both the predator and its prey, the end results are much more realistic and useful in planning potential control programs.

The predator-prey relationship must also take other factors into consideration when they are present, for example, the effect of pesticides or other anthropogenic stressors on their relationship (Guedes et al., 2022). In this framework, Majidpour et al. (2022) studied the sublethal effect of a mixture of thiacloprid + deltamethrin on the demographic parameters of the cotton aphid *Aphis gossypii* Glover (Hemiptera: Aphididae) and two of its main parasitoids – *Aphidius flaviventris* Kurdjumov (Hymenoptera: Aphelinidae) and *Aphidius colemani* Viereck (Hymenoptera: Braconidae). Because the thiacloprid + deltamethrin mixture was shown to impair both the cotton aphid population as well as its parasitoid *A. flaviventris*, its use was disencouraged when *A. flaviventris*, was also present, while, on the other hand, it was deemed to be relatively safe for use when only *A. colemani* wasps where being used as the parasitoid.

The efficiency of biocontrol agents is affected not only by their own population characteristics, but also by the quality of their hosts as well as the nutritional status of the host plants. For example, Salehi et al. (2019, 2020) studied the effect of nitrogen fertilization on the population parameters of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) and the parasitism efficiency of the braconid parasitoid *Habrobracon hebetor* (Say). They showed that both tomato plant cultivars (Kingston and Superstrain-B) were suitable host plants for *H. armigera*, while *H. hebetor* preferred hosts reared on the cultivar Kingston – the cultivar with the highest N level.

8.3 Computer simulation of predator-prey interactions

Yu et al. (2013b) demonstrated that by using computer simulation the optimal interval between releases can be achieved to fill the predation gaps due to the prevalence of nonpredatory stages (egg and pupal stages), while maintaining the predatory capacity of the control agent. Due to the extremely complicated predator-prey dynamics, it is necessary to integrate the life table and predation rate in a computer simulation model to simulate the predator-prey interaction and to predict the optimal time and quantity for releasing predators (Ding et al. 2021). Because female age-specific life tables are incapable of describing the stage differentiation and ignore the male population, computer models based on the female life tables are incapable of generating reliable, realistic results. In order to successfully create a realistic simulation of biological control that is based on life table theory, TWOSEX-MSChart (Chi 2023c), CONSUME-MSChart (Chi 2023a), and TIMING-MSChart (Chi 2023b) are the only tools that should be considered.

9 Suggestions on some demographic subjects

9.1 Equations

Equations are often the backbone of scientific papers. When used, equations should be listed in correct and logical order. Because the age-stage specific survival rate and fecundity are the basic data obtained in life table research, the equations for s_{xj}, f_{xj}, l_x, and m_x should be listed first

$$s_{xj} = \frac{n_{xj}}{n_{0,1}} \tag{9.1}$$

$$m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}} = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{l_x} \tag{9.2}$$

By using the values for s_{xj}, f_{xj}, l_x, and m_x, the net reproductive rate R_0, the intrinsic rate (r) and the finite rate (λ) can be calculated. The following equations can then be presented

$$R_0 = \sum_{x=0}^{\infty} \sum_{j=1}^{k} s_{xj} f_{xj} = \sum_{x=0}^{\infty} l_x m_x \tag{9.3}$$

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{9.4}$$

$$\sum_{x=0}^{\infty} \left(e^{-r(x+1)} \sum_{j=1}^{k} s_{xj} f_{xj} \right) = \sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{9.5}$$

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{9.6}$$

Equations 9.3~9.6 can be listed in any order. Because the life expectancy equation (e_{xj}) is based on s_{xj} and l_x, it must be listed after Equations 9.1. If the precise method is used to calculate the intrinsic rate (Equation 9.5 or 9.6), the equation of the mean generation must be listed after Equations 9.3~9.6 as follows:

$$T = \frac{\ln R_0}{r} = \frac{\ln R_0}{\ln \lambda} \tag{9.7}$$

Because the reproductive value (v_{xj}) is calculated after r has been determined, the equation for v_{xj} must be listed after the equation for the intrinsic rate.

All equations must be provided with proper index range, the following equation is incorrect because the range of age index is missing.

$$\sum e^{-r(x+1)} l_x m_x = 1 \qquad (9.8)$$

9.2   Fitness

Fitness is a frequently used term in biology, ecology, population genetics, and many other fields. Fitness can be considered as the sum of many factors, including the relative ability to adapt to one's environment, the population growth potential under specific conditions, the resistance to environmental factors or anthropogenic stressors (pesticides et al.), the ability to migrate and colonize new habitats, the passive transmission probability, etc. A variety of definitions, equations, and analyses have been used to calculate "fitness" indices. A universally accepted definition of "fitness" along with its associated equation, however, is not yet available. In insect demography, the term fitness has been used to define a multitude of functions, including the ability of insects to adapt to novel situations (Peng et al. 2015), the effect of banker plants on fitness of a pest and its parasitoid (Jandricic et al. 2014), the influence of temperature regimes (Steinbach et al. 2017, Ullah et al. 2022a and b, Ullah et al. 2022), responses arthropods may have to pesticides (Desneux et al. 2007, Abbas et al. 2016, Ullah et al. 2021, Salim et al. 2022), and many others.

Different equations have been used to calculate a population's "relative fitness", including:

$$R_f = \frac{I_{\text{test population}}}{I_{\text{susceptible population}}} \quad \text{(Jia et al. 2009)} \qquad (9.9)$$

$$R_f = \frac{R_{0,\text{selected strain}}}{R_{0,\text{unselected strain}}} \quad \text{(Abbas et al. 2016)} \qquad (9.10)$$

$$R_f = \frac{R_{0,\text{resistant strain}}}{R_{0,\text{susceptible strain}}} \quad \text{(Ullah et al. 2021, Dong et al. 2022)} \qquad (9.11)$$

Jia et al. (2009) used Equation 9.9 to calculate fitness based on population trend index (I). Abbas et al. (2016) used Equation 9.10 to calculate R_f. The population trend index I (Equation 9.9) is actually similar to the net reproductive rate R_0 (Equation 9.10). Ullah et al. (2021) used the age-stage, two-sex life table and Equation 9.11 to calculate the fitness of pesticide resistance in *A. gossypii*; they observed a lower net reproductive rate in the resistant strain and concluded that relative fitness of the resistant strain had decreased. However, the values of r and λ of the resistant strain were significantly higher than that of the susceptible strain. Dong et al. (2022) also used the age-stage, two-sex life table and the same R_f ratio (Equation 9.11); they reported a relative fitness of 0.799 for the resistant strain; however, there were no significant differences between the resistant and susceptible strains in r and λ values.

Naeem et al. (2021) used several equations for "fitness comparison" including "realized heritability", "intensity of selection", "phenotypic deviation". Solid scientific derivation and reasoning are needed to validate the application of their equations.

Because the intrinsic rate r and finite rate λ are the most representative parameters that consider the effects of the survival rate, developmental rate, first reproductive age, fecundity, and proportion of reproductive females, they are the most appropriate parameters for comparing the growth rate of populations. On the other hand, R_0 values, which do not consider the effect of reproductive age should not be used as a parameter for determining fitness. Luo et al. (2022) discussed why R_0 is not a proper parameter for measuring fitness.

9.3   Risk analysis of quarantine pests

Risk analysis is a trendy and widely used term in many fields, e.g., business, medicine, pest management, pest quarantine, etc. However, the definition for risk analysis in business is totally different from that in pest management. To evaluate the risk of an organism being passively or actively introduced into new habitats or quarantine regulation, the adaptative ability of that organism into its new environment or habitat must be critically assessed based on accurate ecological and biological information, e.g., dispersal mechanisms, economic consequences, etc. Among these, information obtained from constructing and interpreting life table data is of utmost importance. This is because the understanding the survival probability and reproductive potential are essential criteria in predicting the adaptative ability of a pest to a new habitat. It is also necessary to include the fertile and infertile bootstrap samples in the evaluation of fitness. The application of life table theory in pest risk analysis, however, remains an underdeveloped field.

9.4   How many significant digits of population parameters should be reported?

Meyer et al. (1986) used *D. pulex* as an example and suggested "the precision for reporting r values should, in most cases, be limited to two significant figures". Some reviewers have also suggested that two decimal points should be sufficient for the intrinsic and finite rates. In most instances, however, $0 < r < 1$. If only two significant figures were reported, the reported r and λ values would not be precise, and may contradict the theoretical relationship between r and λ, i.e., $\lambda = e^r$ or $r = \ln\lambda$. Steinbach et al. (2017) reported that the intrinsic rate values for the Japan, Sudlon, and Sudlon-Tfm strains of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), were 0.24, 0.25, and 0.24 d^{-1}, respectively, while the finite rate of increase was 1.28, 1.28, and 1.27 d^{-1}, respectively. The Japan and Sudlon-Tfm strains

had identical intrinsic rates (0.24 d^{-1}), but their finite rates were different. Similarly, both the Japan and Sudlon strains had the same finite rate (1.28 d^{-1}), but their intrinsic rates were different. To avoid these situations, we recommend that four significant figures (i.e., decimal places) should be reported for the r and λ values.

9.5 What is the proper sample size for life table study?

Government censuses produces the most complete data available for population demography. They are, however, only applicable to human populations. In insect demographic research, an extremely limited number of insects are used in a life table study. Is there a proper or minimum sample size for a life table study of other organisms? Because insects and mites are ectothermic organisms and many of them can adapt to different hosts or host plants, their life history characteristics will vary with a wide assortment of biotic and abiotic factors. Therefore, it is of prime importance to thoroughly understand the biology of the insect species being studied prior to initiating a life table study. It is also necessary to devise an appropriate rearing regime in order to collect reliable life table data. Although it is impossible to define a fixed number as the proper or minimum sample size, we offer the following suggestions: (1) If there is high immature mortality, a greater number of newborns must be used. (2) For parthenogenic populations, the sample size can be smaller than that used for two-sex populations. (3) A preliminary experiment using group- and individual-rearing can be carried out before initiating the life table study. (4) Because the adult longevity and fecundity data are important components of R_0, r, and λ, there should be at least 30 adults (approximately 15 pairs). There are certainly additional criteria that can be considered, many of which may be species specific.

10 A few pertinent debates

10.1 Should age indexed from 0 or 1?

Although the number of life table publications has increased substantially during the past few decades, mathematical life table research actually originated with Leonhard Euler 260 years ago (1760). Bacaër (2011) detailed the history of life table research, although Lewis' important 1942 publication was overlooked in his book. Two major mathematical systems, i.e., calculus (Lotka 1913a, 1913b, Birch 1948) and matrix (Lewis 1942, Leslie 1945), have been used in life table theoretical deductions. The problem of indexing age from 0 or 1 has been discussed for a number of years (e.g., Goodman 1982, Murray & Gårding 1984, Ebert 1985, Murray 1991, David et al. 1995). It is necessary to clarify this point in order to standardize the equations used.

The general form of the Lewis-Leslie matrix is a square matrix with n columns and n rows (see Equations 10.1 and 10.2).

$$M_0 = \begin{bmatrix} f_0 & f_1 & \cdots & f_{n-2} & f_{n-1} \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & \cdots & s_{n-2} & 0 \end{bmatrix} \quad (10.1)$$

$$M_1 = \begin{bmatrix} f_1 & f_2 & \cdots & f_{n-1} & f_n \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & \cdots & s_{n-1} & 0 \end{bmatrix} \quad (10.2)$$

In Equations 10.1 and 10.2, $f_x \geq 0$ and $s_x > 0$ (Lewis 1942). The age-specific fecundity (f_x) is the total number of eggs produced per individual during the age interval $[x, x+1)$, i.e., $x \leq$ age $< x + 1$. The age-specific survival rate s_x is the proportion (or probability) that an individual will survive from age point x to age point $x+1$. In matrix M_0 (Eq. 10.1), the age is indexed from zero and there are n age groups (from age 0 to $n - 1$), while in matrix M_1 (Equation 10.2) the age is indexed from 1 and there are also n age groups (from age 1 to n). Both M_0 and M_1 have n columns and n rows. The characteristic equation of M_0 is Equation 10.3:

$$|M_0 - \lambda I| = \lambda^{n+1} - f_0 \lambda^n - s_0 f_1 \lambda^{n-1} - s_0 s_1 f_2 \lambda^{n-2} - .. - s_0 s_1 ..$$
$$s_{n-3} f_{n-2} \lambda - s_0 s_1 .. s_{n-2} f_{n-1} = 0 \quad (10.3)$$

The characteristic equation of M_1 is Equation 10.4:

$$|M_1 - \lambda I| = \lambda^n - f_1 \lambda^{n-1} - s_1 f_2 \lambda^{n-2} - s_1 s_2 f_3 \lambda^{n-3} - .. - s_1 s_2 ..$$
$$s_{n-2} f_{n-1} \lambda - s_1 s_2 .. s_{n-1} f_n = 0 \quad (10.4)$$

If there are four age groups and the four age-specific fecundities are 0, 1, 2, and 1, and the three age-specific survival rates are 0.5, 1, and 0.5, respectively, M_0 and M_1 can be written as Equations 10.5 and 10.6, respectively,

$$M_0 = \begin{bmatrix} f_0 & f_1 & f_2 & f_3 \\ s_0 & 0 & 0 & 0 \\ 0 & s_1 & 0 & 0 \\ 0 & 0 & s_2 & 0 \end{bmatrix} = \begin{bmatrix} 0 & 1 & 2 & 1 \\ 0.5 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix} \quad (10.5)$$

$$M_1 = \begin{bmatrix} f_1 & f_2 & f_3 & f_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} = \begin{bmatrix} 0 & 1 & 2 & 1 \\ 0.5 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix} \quad (10.6)$$

The characteristic equation of M_0 (Equation 10.5) and M_1 (Equation 10.6) are the same as Equation 10.7:

$$\lambda^4 - 0.5\lambda^2 - \lambda - 0.25 = 0 \quad (10.7)$$

Leslie (1945, page 191) used an equation similar to Equation 10.3 with age indexed from 0 as in the following equation:

$$\lambda^{k+1} - F_0\lambda^k - P_oF_1\lambda^{k-1} - P_0P_1F_2\lambda^{k-2} - \cdots - \left(P_0P_1\cdots P_{k-2}\right)F$$
$$F_{k-1}\lambda - \left(P_0P_1\cdots P_{k-1}\right)F_k = 0 \qquad (10.8)$$

The above discussions show that the age can be indexed from either 0 or 1 and the characteristic equation and the dominant eigenvalue (i.e., the finite rate of increase λ) are the same.

The Euler-Lokta equation can be written as Equation 10.9 or 10.10

$$\sum_{x=0}^{\infty} e^{-r(x+1)}l_x m_x = 1 \qquad (10.9)$$

$$\sum_{x=1}^{\infty} e^{-rx}l_x m_x = 1 \qquad (10.10)$$

In both Equations 10.9 and 10.10, the age-specific fecundity (m_x) is the total number of eggs produced per individual during the age interval $[x,x+1]$, i.e., $x \le$ age $< x + 1$. The age-specific survival rate l_x is the proportion (or probability) that an individual survives from birth to age point x. In Equation 10.9, the age is indexed from zero (i.e., the age of the newborn is 0), while in Equation 10.10, the age is indexed from one (i.e., the age of the newborn is 1). If the same time unit is used as the matrix method and there are four age groups and the four age-specific fecundities are 0, 1, 2, and 1, and the four age-specific survival rates are 1, 0.5, 0.5, and 0.25, respectively, Equation 10.9 and 10.10 can be written as

$$\sum_{x=0}^{3} e^{-r(x+1)}l_x m_x = e^{-r(0+1)}1\times 0 + e^{-r(1+1)}0.5\times 1 + e^{-r(2+1)}0.5\times 2 +$$
$$0.5\times 2 + e^{-r(3+1)}0.25\times 1 = 1 \qquad (10.11)$$

$$\sum_{x=1}^{4} e^{-rx}l_x m_x = e^{-r\times 1}1\times 0 + e^{-r\times 2}0.5\times 1 + e^{-r\times 3}0.5\times 2 + e \qquad 0.25\times 1 =$$
$$0.5\times 2 + e^{-r\times 4}0.25\times 1 = 1 \qquad (10.12)$$

(Equations 10.11 and 10.12 are the same and the same intrinsic rate r can be obtained by using numerical analyses. They are equivalent to Equation 10.7. The x in l_x and m_x is only the age index; however, the x in e^{-rx} and $e^{-r(x+1)}$ is used in the calculation of the intrinsic rate. Because the x in e^{-rx} and $e^{-r(x+1)}$ is an exponent, it plays an important role. Therefore, the first reproductive age is an important factor in determining the value of r (Lewontin 1965).

Equation 10.3 can be rearranged as

$$\lambda^{n+1} = f_0\lambda^n + s_0f_1\lambda^{n-1} + s_0s_1f_2\lambda^{n-2} + .. + s_0s_1..s_{n-3}f_{n-2}\lambda + s_0s_1..s_{n-2}f_{n-1} \quad (10.13)$$

$$1 = \frac{f_0\lambda^n + s_0f_1\lambda^{n-1} + s_0s_1f_2\lambda^{n-2} + .. + s_0s_1..s_{n-3}f_{n-2}\lambda + s_0s_1..s_{n-2}f_{n-1}}{\lambda^{n+1}} \quad (10.14)$$

If λ is replaced with e^r, f_x is replaced with m_x, and $s_0 \cdots s_{x-1} = l_x(l_0=1)$, it becomes the same equation as 10.9.

Some papers use Equation 10.15 with age indexed from 0 and the exponent with $-rx$

$$\sum_{x=0}^{\infty} e^{-rx}l_x m_x = 1 \qquad (10.15)$$

The first two items of Equation 10.15 are $e^{-r\times 0}l_0m_0 = l_0m_0$ and $e^{-r\times 1}l_1m_1 = e^{-r}l_1m_1$. They are different from the first two items of Equations 10.9 and 10.10. The estimated r will differ from Equations 10.9, 10.10, 10.13 and 10.14.

Computer projection can be also used to solve the problem of age indexed from 0 or 1. As time approaches infinity, the simulated population growth rate using the same values of f_x, s_x, l_x, and m_x in the above discussion will approach the values of r and λ based on Equations 10.3, 10.4, 10.9, and 10.10 as the population approaches a stable age-stage distribution. However, if Equation 10.15 is used to calculate r, it will be different from the simulated growth rate as time approaches infinity.

Although the initial age of a life table can be indexed from 0 (Equations 10.3, 10.8 and 10.9) or from 1 (Equations 10.4 and 10.10), using age indexed from 0 will show the s_{xj} and l_x curves beginning from age 0 on the coordinate point (0,1) (Atlihan & Chi 2008, Jha et al. 2012). If the first age is indexed from 1, the curve of l_x will unusually begin on the coordinate point (1,1) (Myers et al. 2005). We strongly suggest using Equation 10.9.

10.2 r or r_m?

Euler (1760) used λ to represent "the population increase per year", which is equivalent to the finite rate of increase, e^r. Because the characteristic equation of a matrix (Equations 10.3 and 10.4) is very long, most scientists use Equations 10.9 or 10.10 for the Euler-Lotka equation. Lotka (1907) termed r as "the rate of natural increase per head" at "the fixed age-distribution". Lotka (1913a) discussed the "stable age-distribution" and referred to r as the "natural rate of increase". In his 1913b publication (Lotka, 1913b), however, used r_m for males and r_f for females (here the non-italic m and f are used according to the original notation of Lotka). Andrewartha and Birch (1954) wrote "We define r_m, the innate capacity for increase, as the *maximal* rate of increase attained at any particular combination of temperature, moisture, quality of food, and so on, ….". Computer projection using the age-stage, two-sex life tables showed that as time approaches infinity, the growth rate of the total population and all life stages will approach the stable growth rate, i.e., the intrinsic rate (Equation 10.16) and the finite rate (Equation 10.17), and that the population approaches a stable age-stage distribution (Akca et al. 2015, Saska et al. 2016, Bussaman et al. 2017, Huang et al. 2018, Chi et al. 2020, Luo et al. 2022). The curves representing stage sizes in log scale will approach linearity and their slopes will be the logarithm of λ:

$$r_{j,t} = \ln\left(\frac{n_{j,t+1}+1}{n_{j,t}+1}\right) \xrightarrow{t\to\infty} \ln\left(\frac{n_{j,t+1}}{n_{j,t}}\right) = \ln\left(\frac{n_{total,t+1}}{n_{total,t}}\right) \quad \ln$$

$$= \ln\left(\frac{\lambda \cdot n_{total,t}}{n_{total,t}}\right) = \ln \lambda = r \tag{10.16}$$

$$\phi_{j,t} = \log\left(\frac{n_{j,t+1}+1}{n_{j,t}+1}\right) \xrightarrow{t\to\infty} \log\left(\frac{n_{j,t+1}}{n_{j,t}}\right) = \log\left(\frac{n_{total,t+1}}{n_{total,t}}\right) \quad \log$$

$$= \log\left(\frac{\lambda \cdot n_{total,t}}{n_{total,t}}\right) = \log \lambda \tag{10.17}$$

where $n_{j,t}$ is the number of individuals in stage j at time t, $r_{j,t}$ and $\phi_{j,t}$ is the growth rate of stage j at time t, $n_{total,t}$ is the total population size at time t.

The simulated population growths of *Acrythosiphon pisum* (Harris) (Hemiptera: Aphididae) and *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) are

shown in Fig. 12. The growth rate of all life stages of *A. pisum* approached the intrinsic rate ($r = 0.2080$ d^{-1}) (Fig. 12A), and the stage structure approached a stable stage distribution with all stage curves forming an identical slope (log$\lambda = 0.0904$) (Fig. 12B). However, in the population having a slower growth rate (e.g., in *F. occidentalis*, $r = 0.0785$ d^{-1} and $\lambda = 1.0816$ d^{-1}), the population growth rate did not settle down to the intrinsic rate (Fig. 12C) and the stage structure did not approach the stable stage distribution (Fig. 12D). Before a population settles down to the stable age-stage distribution and stable growth rate, there will be obvious fluctuations and the growth rate may be greater or less than the stable growth rate. Thus, r and λ is the "stable" growth rate, and should not be defined as the "maximal" rate.

Different symbols have been used to designate the intrinsic rate, with the most common of these being r and r_m. It is not necessary to search the literature for the origin of different symbols and definitions, we suggest using r for the intrinsic rate.
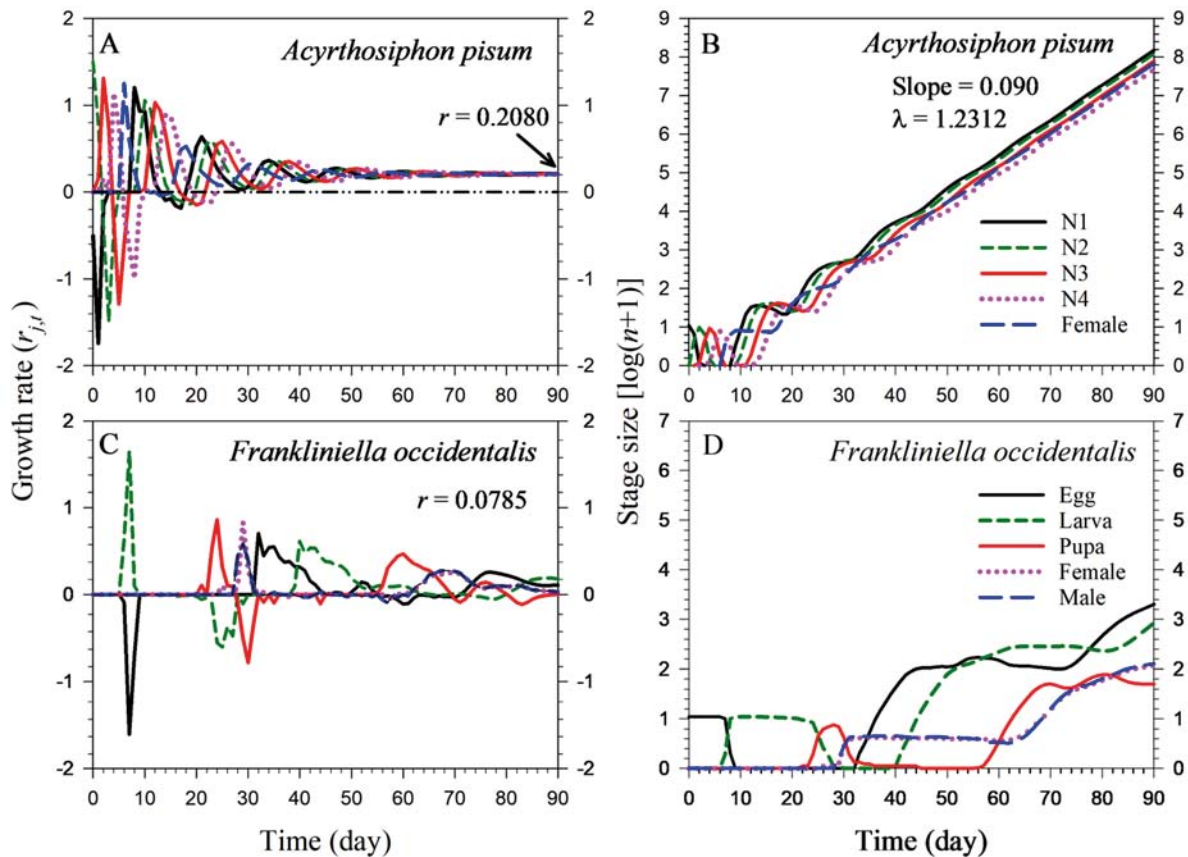

Fig. 12. Population growth rates and stage sizes of *Acyrthosiphon pisum* ($r = 0.2080$ d^{-1}, $\lambda = 1.2312$ d^{-1}) and *Frankliniella occidentalis* ($r = 0.0785$ d^{-1}, $\lambda = 1.0816$ d^{-1}). **A.** The growth rate of all life stages of *A. pisum* approached the intrinsic rate. **B.** The sizes of all life stages of *A. pisum* approached the stable age-stage distribution and all stage curves approached the same slop (log$\lambda = 0.090$) after 60 d. **C.** The growth rate of *F. occidentalis* did not approach the intrinsic rate. **D.** The stage structures of *F. occidentalis* did not approach the stable stage distribution within 90 d.

10.3 Simplified equations should not be used

Before personal computers were readily accessible, several simplified equations were proposed to overcome the difficulty in calculating the intrinsic and the finite rates (e.g., Howe 1953, Hughes 1962, Laughlin 1965, Wyatt & White 1977, Janssen et al. 2022). The issues associated with using simplified methods have been repeatedly discussed, e.g., Carter et al. (1978), Vranken & Help (1983), Mirmohammadi et al. (2009), Chi et al. (2020), Saska et al. (2021).

Some simplified methods estimated the mean generation time (T) first, after which the intrinsic rate (r) was calculated. However, Dublin & Lotka (1925) wrote "In the exact computation this process is reversed, and exact value for r being first obtained, and from this is deduced the exact value of T, in complete accord with the definition of this quantity".

We strongly advise against using these and future over-simplified equations. If saving time, labor, and/or research funds in life table research is necessary, researchers should, instead, consider using larger time units (intervals) (Zheng et al. 2016), group-rearing (Chang et al. 2016), and the boot-strap match technique (Amir-Maafi et al. 2022). These time-saving procedures can be successfully used to collect life table data without compromising scientific theory.

10.4 Jackknife method should not be used

Chi & Yang (2003) pointed out that application of jackknife will result in discrepancy between the estimated means of population parameters and their theoretical definitions. Huang & Chi (2013) mathematically invalidated using the jackknife method in life table research. Although Yu et al. (2013b) demonstrated that the jackknife technique can generate results that are contradictory to life table theory, the jack-knife method is still frequently used (Jandricic et al. 2014; Maia et al. 2014). The problem with using the jackknife method is often noticed in erroneous relationships occurring between R_0 and r, or between R_0 and λ. Over a hundred years ago, Lotka (1913b) gave the relationship between the intrinsic rate and the net reproductive rate as "$r \gtrless 0$ according as $\int_0^\infty p_m(a)\beta_m(a)\,da \gtrless 1$." Later, Lewis (1942) stated that the equivalent relationship between the net reproductive rate and the finite rate as "a net reproduction rate $\gtrless 1$ means $l \gtrless 1$ and vice versa, but the magnitudes of the two measures will be different." When the jackknife method is used, it may result in contradictory results. Prado et al. (2009) reported that $R_0 = 1.17 > 1$, but $r = -0.01 < 0$ for *Nezara viridula* L. (Hemiptera: Pentatomidae) ([Table 1](#) in Prado et al. 2009). Khatri et al. (2017) stated that $R_0 = 0.33 < 1$, but $r = 0.0405 > 0$ for *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) ([Table 1](#) in Khatri et al. 2017); Peng et al. (2020) calculated that $R_0 = 0.97 < 1$, but $r = 0.016 > 0$ and $\lambda = 1.10 > 1$ for *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae) ([Table 2](#) in Peng et al. 2020). Bonser et al. (2022) reported $R_0 = 31.9$, $r = 0.025$, $\lambda = 0.5$, $DT = -14.2$ for *Chrysodeixis includens* (Walker) (Lepidoptera: Noctuidae) ([Table 4](#) of Bonser et al.

2022). These published disparities exemplify why it is necessary to avoid the jackknife method in life table analyses.

10.5 Stage-structured and size-structured models

Bodenheimer (1938) mentioned in his book "Problems of Animal Ecology" that topics focused on diapause and sex and associated problems had largely been neglected in published experiments, observation and analysis. Because the data sampled from field studies was concerned primarily with stage or size, and not age, several models have been proposed for the analysis of these kind of data; e.g., the stage-structured population (Lefkovitch 1965, Caswell 1983, Manly 1990) and size-structure population (Ebenman & Persson 1988). Lefkovitch (1965) tried to deal with the problem "the variation of the duration of the stage that different individuals may show". This oversight has been successfully resolved in the age-stage, two-sex life table (Chi & Liu 1985, Chi 1988, Chi et al. 2020). Chi & Yang (2003) showed that if there are variable developmental rates among individuals and the life history raw data is organized according to the model used by Caswell (1983, 2001), the results will be similar to those obtained using adult age, because Caswell's model classifies individuals by age within stages.

10.6 Avoid fitting curve to an equation without mathematical reasoning

Recently, Chi et al. (2020) suggested that researchers should "Resist the temptation to fit data into beautiful curves". Atlihan et al. (2017) and Tuan et al. (2017) demonstrated that fitting the age-specific survival curve (l_x) to a Weibull function may result in errors. This is especially true where there is higher mortality in specific stages. Unfortunately, we believe that curve fitting will remain a common practice because many scientists are accustomed to those equations. Ricklefs (1990) noted that "Lotka was quick to point out that blind application of equations like the logistic was meaningless and potentially misleading unless one understood the biological processes responsible for the behavior that one could describe mathematically." (in Ricklefs (1990), Ecology, 3rd Edition, 1990, p. 330). Although we been unable to locate that precise original text from Lotka's numerous important publications, we do strongly agree with the statement.

11 Conclusion

Overall, the age-stage, two-sex life table is a prime tool in population ecology studies and pest management programs (Baral & Jha 2018, Chi et al. 2020) and has been widely adopted for use in diverse aspects of demographic research. Due to the problems inherent in the female age-specific life table, i.e., traditional female-based, age-specific life tables completely ignore the effects attributable to the male population and are inherently unable to differentiate between the developmental

stages that are characteristic of an insect's growth process (Huang & Chi 2012, Huang et al. 2018, Chi et al. 2020), the female age-specific life table should not be used.

Knowledge of the theoretical background of a science is critical for its proper application. An understanding of the age-stage, two-sex life table and its various components (Chi & Liu 1985, Chi 1988, Huang et al. 2018, Chi et al. 2020) is essential to properly apply the TWOSEX-MSChart program. Unfortunately, fundamental errors have been observed in several publications using the age-stage, two-sex life table and the TWOSEX-MSChart; e.g., equations were listed in incorrect order, errors in the equations, a death rate greater than one, errors in figures, and more. We have discussed some of these errors in Section 10. Moreover, there are special, atypical cases, e.g., populations with arrhenotokous reproduction (Tuan et al. 2016) or physogastric reproduction (Bussaman et al. 2017), complicated host feeding behavior (De Bona et al. 2023), etc., that require further study in both life table theory and application. Not only is the data analysis in these cases different from the norm, but the methods used in population projection also differ.

Many special cases have already been encountered and solved in life table studies: including, (i) female and male individuals having different developmental stages, (ii) some individuals entering diapause, with others developing normally, (iii) individuals having different number of immature stages, (iv) methods of calculating the contribution different morphs make to the population parameters (Lin et al. 2023), etc. It is impossible to cover all of these in this review. There are user manuals for proper data analysis of these special cases available at http://140.120.197.173/ecology.

Although the age-stage, two-sex life table theory is well developed and there are accompanying user-friendly programs (TWOSEX-MSChart, CONSUME-MSChart, and TIMING-MSChart) available for free downloading, the practical applications involving life tables, predation rate, mass-rearing, computer simulation, etc. are far from being fully exploited.

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