Advantage and reasons of using the age-stage, two-sex life table

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Life tables are the most ancient and important tool in demography. They are widely used for descriptive and analytical purposes in demography, public health, epidemiology, population geography, biology and many other branches of science. -- Vladimir M. Shkolnikov

Life tables are the basis of ecology. But…

Until recently, the application of life tables to the study of insect populations for pest management has been underutilized and underemphasized due to the difficulties involved in data collection and the variability of life tables generated under different environmental conditions and/or different host plants.

Life tables are the basis of ecology. But…

These problems can also be partially attributable to **the recurrent use of the more traditional female age-specific life tables** (Lewis 1942; Leslie 1945; Birch 1948; Carey 1993). These life tables not only disregard the contribution of the **male component** of the population, but are also **incapable of correctly differentiating between the different developmental stages** which are unique to insect and most other arthropod populations.

In your paper, you have to point out

- The problem of applying female age-specific life tables to insect populations
- The main **differences** between the age-stage, two-sex life table and traditional life tables
- The **advantages** of the age-stage, two-sex life table
  (Please see Chapter 2)

Is "population" only for ecology?

- The physiology of cold hardiness, the supercooling points and diapause.
- The effect of neem seed oil on survival and development of insects.
- Effect of climate change and global warming.
- Effect of sublethal concentrations of chlorpyrifos on three successive generations of *Daphnia carinata*
- Effect of transgenic Cry 2Ab tomato plants on *Helicoverpa armigera* (Hübner)

Most Research should focus on population level

- To take the variable response among individuals into consideration
- To detect the overall effect on the survival, growth, and reproduction of a population (Population Health, i.e., Human Public Health)
- To determine the long-term effect (entire life span) into consideration (not one age or single stage). Only then we can predict or simulate the long-term effect.
- Conservation strategies: Population and species levels

Life table, why?

- A life table is based on solid, robust, and mathematical theory
- It covers the entire life span
- It describes stage differentiation
- It can be used to project population growth
- It takes into consideration the differences in behavior, susceptibility to pesticides, vulnerability to predators, …

Life table, why?

- Developmental rate
- Survival rate
- Fecundity
- Sex ratio
- Stage differentiation
- Variation among individuals
- Whole life span
- Mathematical theory
- Wholeness: developmental rate from egg to adult. Stages are not isolated data.
- Variation among stages: susceptibility to abiotic factors, pesticides, etc.
- Population project is possible (with consideration of all factors.)

Life table

Development, survival, fecundity, sex ratio, age, stage, stage differentiation, are integrated in life table theory and in data analysis. Integration makes also a rational and complete statistical analysis.

Age-stage, two-sex life table. Why?

Advantages to Using the Age-Stage, Two-sex Life Table

- All individuals are included in analysis. No assumption of "1:1" sex ratio.
- We don't use "adult age".
- We accurately describe the stage differentiation and stage overlapping.
- We accurately include "preadult mortality".
- We proved relationship between F and R_0.
- We include male predators in biological control.
- …………………

Solid relationship between F and R_0

Chi (1988) determined the relationship between F and R_0 as

$$R_0 = F \times \frac{N_f}{N}$$

where N is the total number of eggs used for the life-table study at the beginning and N_f is the number of female adults that emerged.

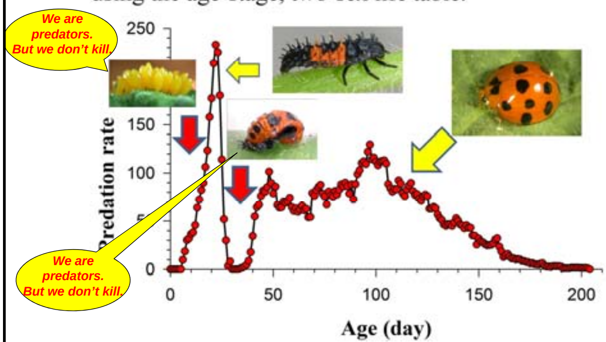
Stage differentiation is beautiful and important

- The stage differentiation can be taken into consideration (stage grouping is important)
  - Variations in behavior and physiology, ecology, and susceptibility to pesticide are important
  - Eggs are susceptible to egg parasitoids.
  - Larvae can cause damage, but pupae don't.
  - Adult females can produce eggs.

Stage differentiation is important

Insects and mites are age-stage-structured. Stage differentiation is important to insect physiology, biochemistry, ecology, etc., and is essential when trying to **quantify the damage** caused by a pest population or the **control efficacy of a predator population**.

An accurate description of the survival, development, and predation capacity of a predator can be achieved using the age-stage, two-sex life table.



Biological Control (2013) 64: 1-9.

Stage overlaps can be observed

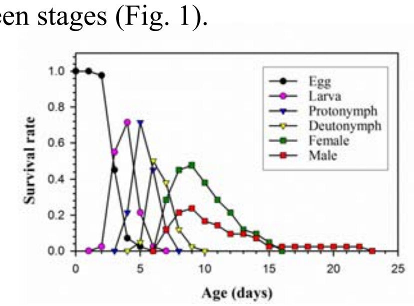
- The stage overlaps can be accurately and truly described.
  - It is not necessary to use the means of stage duration to divide the life history into stages.
  - The age-stage survival rates calculated by using the age-stage, two-sex life table are exactly the same as your daily records of age-stage and sex structure of the cohort.

Preadult mortality can be correctly described and analyzed

- Precise preadult mortality can be included
  - Preadult mortality affects the l_x
  - It is difficult, however, to sex individuals who have died in the preadult stages.
  - If you use an age-specific female life table, you will have to confront the problem of determining how many of the dead individuals are female.
  - If you assume a 0.5 sex ratio and there is a single dead individual in the preadult stage – should it be included or not?

Stage differentiation and overlap

Because the development rate varies among individuals, there is always obvious overlapping between stages (Fig. 1).



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Population projection with stage structure

- Because the age-stage, two-sex life table can take the stage differentiation into consideration, it can be used to simulate the effect of stage-specific mortality properly, while the female age-specific life table is incapable of doing this.
- Population projection based on the age-stage, two-sex life table can simulate the population growth during pesticide applications.

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The male population is included and sex ratio can be analyzed

- The male population is included
  - Male predators also contribute to the predation
  - Male prey can be used as food
  - Males can also cause economic damage
  - There are many differences between males and females (longevity, survival rate, predation rate, consumption rate, pesticide susceptibility, …)

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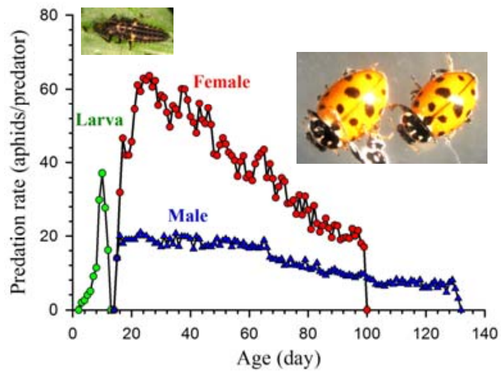
Both sexes are important.



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Effect of sex ratio

Because the age-stage, two-sex life table includes both sexes, the effect of sex ratio on the population parameters can be taken into consideration when the bootstrap method is used. However, if a female only life table is used, the effect of sex ratio is totally ignored.

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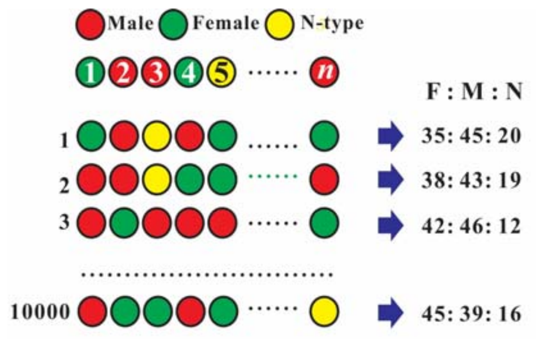
Bootstrap reveals variability of sex ratio



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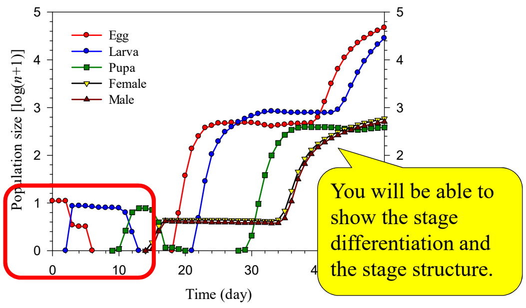
Population projection shows stage differentiation

If you include population projection in your paper, you can write "Because the age-stage, two-sex life table is capable of describing the stage differentiation, population projection based on life tables can reveal the details of population growth and the stage structure (Fig. x)."

Population Projection by using TIMING-MSChart



Please modify or rephrase all statements according to your insect, data, your idea and ….

You have to face editor and reviewers

- Not every editor and reviewer understands life tables. Most editors and reviewers may have only limited knowledge about traditional female age-specific life tables.
- A few journals are not interested in "life table **only**" papers.
- Your main subject is pest management, biological control, insect physiology, toxicology, etc. To most entomologists, life tables are only a tool, but they are an important tool.

You can use life tables in many studies

- Life tables on different host plants
- Life tables at different temperatures
- Life tables of different ecotypes
- Life tables of resistant and susceptible populations
- Life tables of invasive species
- Life tables under elevated CO_2
- Life tables of predators on different preys
- ……

But, it is not necessary to use "life table" in your title

- Survival and development of … on different host plants
- Effect of temperature on the fitness of ….
- Different ecotypes
- Survival and fecundity of resistant and susceptible populations
- Prediction of invasive species
- Global warming …
- Effect of prey species on the survival of predator

Differences

Female age-specific
- Female individuals only
- Stage differentiation is ignored
- No relationship between mean fecundity (F) and net reproductive rate (R_0)
- Effect of sex ratio is ignored
- ……

Age-stage, two-sex
- All individuals
- Stage differentiation can be precisely described
- Mathematically verified: $R_0 = F\ (N_f/N)$
- Effect of sex ratio and immature mortality on r, R_0, λ and T is included
- ……

Problems of applying a female age-specific life tables to insect populations

Errors are often observed in papers based on female age-specific life tables. Errors demonstrate the **insufficiency, incompleteness, and inaccuracy of female age-specific life tables.**
這些常見錯誤顯示傳統雌性年齡生命表的不足、不完整與不正確。

Preadult mortality cannot be properly included

- Preadult mortality affects the l_x
- It is difficult, however, to sex individuals who have died in the preadult stages.
- If you use an age-specific female life table, you will have to confront the problem of determining how many of the dead individuals are female.
- If you **assume** a 0.5 sex ratio and there is a single dead individual in the preadult stage – should it be included or not?

Erroneous relationship between R_0 and r

- Lotka (1913, p. 293) stated "In the first place it can be seen by inspection, that r >=< 0 according as $\int_0^\infty p_m(a)\beta_m(a)da >=< 1$."
- Lewis (1942) also proved that $R_0 >\leq 1$ means $\lambda >\leq 1$ and *vice versa.*
- Errors may be observed when the age-specific female life table is applied to a two-sex population.

Erroneous relationship between R_0 and F

- According to the mathematical proof in Chi & Su (2006), the relationship between the female mean fecundity (F) and R_0 in the female age-specific life table should be $R_0 = s_a \cdot w \cdot F$.
- Yu et al. (2005) and Chi & Su (2006) gave a detailed discussion and mathematical proofs on the possible problems in application of the female age-specific life table to a two-sex population and the problem of l_x and m_x based on adult age.

Erroneous relationship among R_0 and GRR

- The relationship among GRR, R_0, and the preadult survival rate (l_a) was proven to be $R_0 < l_a \cdot GRR < GRR$.
- However, when applying the female age-specific life table to a two-sex population, due to the difficulty in determining the preadult mortality of the females, the calculated age-specific survival rate and fecundity are possibly incorrect and consequently the relationship among GRR, R_0, and l_a may also be incorrect.

Use of "adult age" results in errors

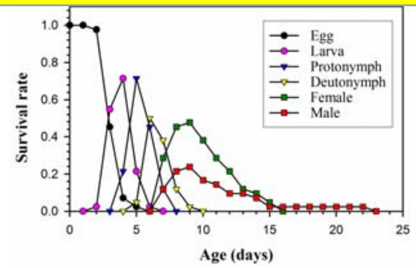
- If one used the "adult age" to construct the life table, they would be unaware of the improper manipulation of the survival and fecundity curves (l_x and m_x). Consequently, the interpretation of demographic traits based on an "adult life table" would result in a variety of problems.

Stage differentiation is ignored

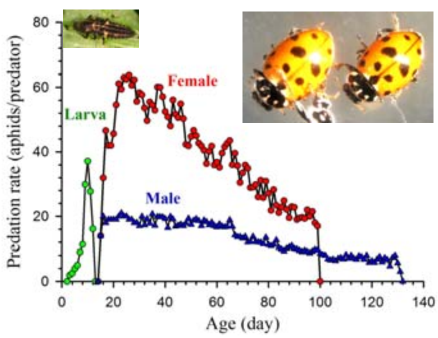
Insects and mites are age-stage-structured. Stage differentiation is important to insect physiology, biochemistry, ecology, etc., and is essential when trying to **quantify the damage** caused by a pest population or the **control efficacy of a predator population**.

However, stage structure is important!

We should not ignore the stage overlap time periods.



Both sexes should be included in data analysis and application



Effect of sex ratio is totally ignored

- In the female age-specific life table, fecundity (m_x) is usually calculated by dividing the total eggs laid by all survived females of "adult age" x and **assuming** a 1 : 1 sex ratio for all eggs.
- Sex ratio plays an important role in the development of the population, the theory of sexual selection, evolution, etc.
- **However, if a female only life table is used, the effect of sex ratio is totally ignored.**

Problems with using a female age-specific life table

Female age-specific

~~M,7,4,4,4,15,53~~
F,5,6,4,5,7,34
~~M,7,4,4,5,14,48~~
F,7,4,4,5,14,96
F,7,5,3,6,14,79
~~M,7,5,4,5,14,74~~
~~N,7,3,-2~~
~~N,7,-4~~ ?
~~N,6,-8~~

- Males are ignored
- Stage grouping is impossible
- Stage overlapping is ignored
- Fecundity curve based on adult age results in errors
- Effect of sex ratio is ignored.
- ……

Things you should not do

Things you should not do

- Don't use simplified methods. It is 2016!
- **Use *r*. Don't use r_m!**
- Don't use Jackknife method.
- Don't use "adult age".
- Don't fit l_x or m_x to any model unless you can give good reasoning.
- Don't use line chart.
- Don't use smooth lines for l_x or m_x.

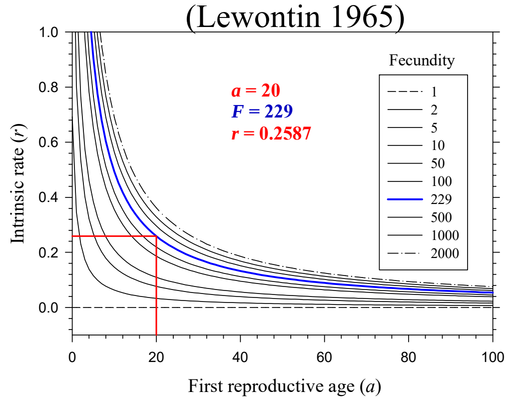
Using the mean fecundity (*F*), the age of the first offspring (*a*), and the preadult survival rate (l_a) to critically examine the intrinsic rate

$$e^{-r(a+1)}F \cdot l_a = 1$$

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

J. Econ. Entomol. 1–13 (2015); DOI: 10.1093/jee/tov187 **(Forum)**

Effect of first reproductive age on *r* (Lewontin 1965)



Good interpretation, new ideas, good topics and questions

You are welcome to use all new ideas you learned in my lecture in your research or thesis.

Using hatched eggs in the life table, why?

- Parent cohort is a small sample! Is the hatch rate of parent cohort the hatch rate of the real "population"?
- Newly emerged and old females may produce unfertilized eggs.
- Some insects produce **"trophic eggs".**

(This part is published in Journal of Applied Entomology).

Can you apply the age-stage, two-sex life table to parthenogenetic populations?

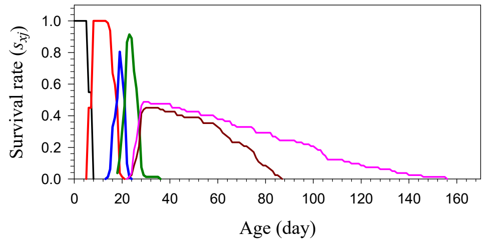
Yes. To show the stage differentiation of female parthenogenetic populations (aphids and others), you should use the age-stage, two-sex life table. Otherwise you cannot describe the stage structure properly.

Reviewer's suggestion

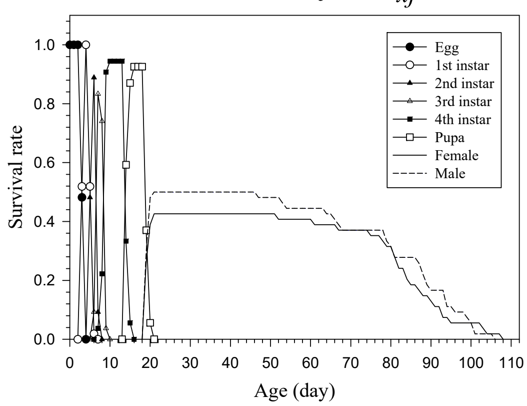
- I suggest authors to include the statistical analysis on age-staged survivorship between the two host plants so as to target the bottle neck for making management activities, since age-staged survivorship of *S. litura* from Fig 2 were not statistically indicated.

What is s_{xj}

The s_{xj} is the probability that a newly born individual will survive to age x and stage j. Each curve is formed due to the survival, stage differentiation, developmental rate, and stage duration. Therefore, it can exactly describe the death, the beginning and end of a stage, etc.



How to analyze s_{xj}



Factors affecting s_{xj}

- Beginning age x of the survival curve of stage j
- Last age x of the survival curve of stage j
- Mortality of stage j
- Death age of individuals that died in stage j
- Mean duration of stage j
- You can compare every factor as Lewontin (1965) compared the beginning, peak, and end of reproduction by using bootstrap results.

Answer to reviewers' comments

- Because the shapes of the survival curves (s_{xj}) are determined by many factors, the beginning and end of the stage survival curves, the peak of the stage emergence, the total stage-specific mortality, the age distribution of the dead individuals, we compared each factor based on the bootstrap results.
- The overall effect of survival and reproduction is demonstrated by the r and λ.

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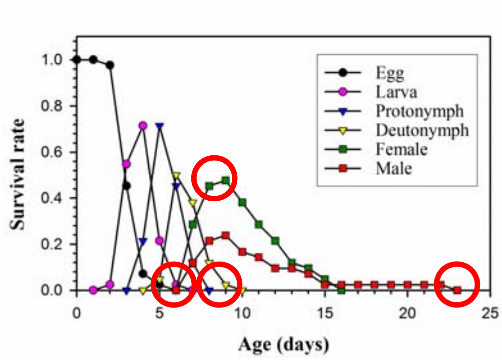
Analysis of survival curve



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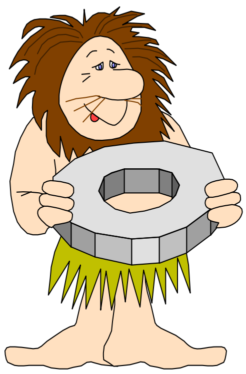

Teşekkür ederim!

سپاسگزارم

謝謝!

ขอบคุณครับ

Děkuji

Danke!

¡Muchas gracias!

Thank you!

ご清聴ありがとうございます！

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