Title: Life Tables of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae): with a Mathematical Invalidation for Applying the Jackknife Technique to the Net Reproductive Rate

Running title: Life table and jackknife technique

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Abstract

1. Life table data for the melon fly, *Bactrocera cucurbitae* (Coquillett), reared on cucumber (*Cucumis sativus* L.) were collected under laboratory and simulated field conditions.

2. Means and standard errors of life table parameters were estimated for two replicates using the jackknife technique.

3. At 25°C, the intrinsic rates of increase (*r*) found for the two replicates were 0.1354 and 0.1002 day\(^{-1}\), and the net reproductive rates (*R*_0) were 206.3 and 66.0 offspring, respectively.

4. When the cucumbers kept under simulated field conditions were covered with leaves, the *r* and *R*_0 for the two replicates were 0.0935 and 0.0909 day\(^{-1}\), 17.5 and 11.4 offspring, respectively. However, when similar cucumbers were left uncovered, the *r* and *R*_0 for the two replicates were 0.1043 and 0.0904 day\(^{-1}\), and 27.7 and 10.1 offspring, respectively.

5. Our results revealed that considerable variability between replicates in both laboratory and field conditions is possible; this variability should be taken into consideration in data collection and application of life tables.

6. Mathematical analysis has demonstrated that applying the jackknife technique results in unrealistic pseudo-*R*_0 and overestimation of its variance.

7. We suggest that the jackknife technique should not be used for the estimation of variability of *R*_0.

Key words. *Bactrocera cucurbitae, Cucumis sativus*, life table, net reproductive rate, jackknife method.
Introduction

The melon fly, Bactrocera cucurbitae (Coquillett) (Diptera: Tephritidae), has been one of the most important pests in Taiwan (Huang & Chi, 2011), and in many other regions in Asia (Koyama et al., 2004; Dhillon et al., 2005) for several decades. Although the agricultural agencies have invested heavily in research, workshops, and control measures related to the fly, it remains a major pest in Taiwan (Huang & Chi, 2011). For sustainable pest management in organic farming, it is crucial to develop a comprehensive understanding of the population ecology of the target pests. Life table studies should be the first priority in ecologically sound pest management programs because only life tables can provide the most detailed and correct descriptions of the survival, stage differentiation, and reproduction of populations. Age-specific female life tables of B. cucurbitae were developed by Vargas et al. (1996, 1997, 2000) and Yang et al. (1994). However, the theories relating to female age-specific life tables (Lewis, 1942; Leslie, 1945; Birch, 1948) address only female populations and ignore male populations. Chi & Liu (1985) and Chi (1988) observed that female age-specific life tables cannot correctly describe the growth and stage differentiation of insect and mite populations. Thus, although numerous female life tables have been published for many insect species, their practical applications are quite limited. Huang & Chi (2011) reported the first age-stage, two-sex life table for B. cucurbitae under laboratory conditions with cucumber slices as the rearing medium. They demonstrated that an erroneous relationship is obtained if an age-specific female life table is applied to a two-sex population. Furthermore, they indicated that the study of life tables constructed under field conditions can be helpful by revealing differences between the values of population parameters in the field and in the laboratory.
Liquido (1991) demonstrated that fallen fruits on the ground act as a reservoir for melon fly populations. To construct precise predictions of the dynamics of populations in the field, it is necessary to identify the differences between life tables collected in the laboratory and those actual life tables under field conditions. On the other hand, due to the tedious and time-consuming work of life table studies, most life table studies are carried out by using single cohort without replication. To estimate the means and variances of population parameters obtained from a single cohort, jackknife technique is widely used. Meyer et al. (1986) used jackknife and bootstrap techniques in estimating uncertainty in intrinsic rate and concluded that jackknife was more cost-effective based on simulation. Efron & Tibshirani (1993) discussed the failure of jackknife. Chi & Yang (2003) pointed out that application of jackknife will result in some degree of discrepancy between the estimated means of population parameters and their theoretical definition. When we use the jackknife method to estimate the mean value of the net reproductive rate, we often obtain some pseudo-\(R_0\) value of zero. An mathematical explanation is needed to justify or falsify the use of jackknife technique. In this study, eggs of melon flies were artificially introduced into whole cucumbers (\textit{Cucumis sativus} L.), then kept at 25°C and under field with replications. Life tables were constructed and the population parameters were measured for replicates. Furthermore, we derived a mathematical proof to demonstrate the problem of the jackknife method for the estimation of the mean and standard error of the net reproductive rate.

\section*{Materials and methods}

\subsection*{Life Table Study}

Melon flies were collected in a field used to grow vegetables and subsequently
reared on cucumber (*Cucumis sativus* L.). The colony was maintained in the
laboratory of the Department of Entomology, National Chung Hsing University
(Taichung, Taiwan) for two generations before the beginning of the life table study.
For the life table study, eggs laid within 24 h were collected using piled cucumber
slices following the method of Huang & Chi (2011). For implanting eggs into the
cucumber, a pyramid-shaped hole with a rectangular base (1.5 cm each side, 1.5 cm
height) was cut with an arrowhead-shaped knife. Twenty eggs were placed in the
hole with a fine writing brush. Before the pyramid-shaped cucumber piece was
replaced, its tip was removed to leave a space for the eggs. To study the cohort life
tables at 25°C, five cucumbers with eggs were kept in a plastic jar (26 cm height, 23
cm diameter) with loamy soil. The mouth of the jar was covered with fine mesh net
and kept at a constant temperature of 25°C in a growth chamber under a photoperiod
of 12:12 (L:D) h. To study the life table under field conditions, five cucumbers with
eggs were placed in a jar, kept in a shaded area and covered with dried mango leaves.
Another five cucumbers with eggs were placed in a jar and kept under direct sunlight
in the field with no leaf cover. The field study was conducted from 5 June to 9
September 2006. The average field temperature was 28.1°C. Two replicates were
used for each treatment. The numbers of emerged adults were observed, and pairs of
adults were formed. The eggs laid daily by the melon flies were collected on sliced
cucumber as described in Huang & Chi (2011).

Demographic Analysis

The life history data were analyzed according to the age-stage, two-sex life table
theory (Chi & Liu, 1985) and the method described by Chi (1988). The means and
standard errors of the life table parameters were estimated with the jackknife method
(Sokal & Rohlf, 1995). The population parameters estimated were the intrinsic rate of increase \((r)\), the finite rate of increase \((\lambda)\), the gross reproductive rate \((GRR)\), the net reproductive rate \((R_0)\) and the mean generation time \((T)\). In this paper, the intrinsic rate of increase is estimated with the iterative bisection method from the Euler-Lotka formula

\[
\sum_{x=0}^{\infty} e^{-r(x+1)}l_xm_x = 1
\]

with age indexed from 0 (Goodman, 1982). The mean generation time is defined as the length of time that a population needs to increase to \(R_0\)-fold of its size (i.e., \(e^T = R_0\) or \(\lambda^T = R_0\)) at the stable age-stage distribution and is calculated as \(T = (\ln R_0)/r\). The age-stage life expectancy \((e_{xj})\) is calculated according to Chi & Su (2006). To facilitate the tedious process of raw data analysis, a computer program TWOSEX-MSChart for the age-stage, two-sex life table analysis (Chi, 2010) in Visual BASIC (version 6, service pack 6) for the Windows system is available at http://140.120.197.173/Ecology/ (Chung Hsing University) and at http://nhsbig.inhs.uiuc.edu.tw/www/chi.html (Illinois Natural History Survey). We used a Tukey-Kramer procedure (Dunnett, 1980) to compare the difference among treatments following the description of Sokal & Rohlf (1995).

Results

Life Table of *B. cucurbitae*

The developmental times for each stage are listed in Table 1. At 25 °C, the duration of the preadult stage in whole cucumber was 17.8 and 18.5 d (two replicates). This value was much greater than the corresponding value for growth in cucumber kept under field conditions with or without leaf coverage. The adult
pre-ovipositional periods (APOP) in the different treatments ranged from 7.0 to 9.1 d. There were no significant differences among these values. The total pre-ovipositional period (TPOP) at 25°C was, however, significantly longer than those found in the field. The adult longevities of both male and female adults at 25°C are also longer than those observed under field conditions. The total fecundity varied significantly among treatments (Table 2). Significantly higher fecundities (859 and 660 eggs/female) were observed in females reared at 25°C than in females emerged under field conditions. The high coefficients of variation (CV) of mean fecundities showed the high reproductive variability among individuals.

The detailed age-stage survival rates \((s_{ij})\) of \(B. cucurbitae\) for the different treatments are plotted in Fig. 1. The parameter \(s_{ij}\) is the probability that a newborn will survive to age \(x\) and stage \(j\). The survival rate curves of \(B. cucurbitae\) cohorts vary significantly between replicates for populations reared in whole cucumbers. In general, the survival rate in the laboratory is higher than in the other treatments. At 25°C, cohorts in the laboratory survived longer than those in the field. This difference is also evident from the longer developmental time of the preadult stage and from the adult longevities (Table 1).

The daily mean number of offspring produced by individual \(B. cucurbitae\) of age \(x\) and stage \(j\) per day is shown with the age-stage fecundity \((f_{ij})\) in Fig. 2. Because only adult females produce offspring, there is only a single curve \(f_{A2}\) (i.e., the adult female is the second life history stage). The age-specific survival rate \((l_x)\) and the age-specific fecundity \((m_x)\) are also plotted in Fig. 2. The \(l_x\) curve describes the change in the survival rate of the cohort with age. Significant variability can be observed between the two replicates. In one replicate at 25°C, more than 40% \(B. cucurbitae\) survived to the adult stage, but the corresponding value in another
replicate was much smaller, approximately 20%. However, at 25°C, the survival rates in the laboratory are higher than those in the field (Fig. 2).

Population Parameters

The means and standard errors of population parameters of *B. cucurbitae* in the different treatments investigated are listed in Table 2. For the eggs artificially placed in cucumber and kept at 25°C, the intrinsic rates of increase (r) found for the two replicates were 0.1354 and 0.1002 day\(^{-1}\), the net reproductive rates (\(R_0\)) were 206.3 and 66.0 offspring, and the mean generation times (\(T\)) were 39.5 and 42.6 days, respectively. For the cucumbers kept in the field and covered with leaves, the population parameters (\(r, R_0\) and \(T\)) were 0.0935 and 0.0909 day\(^{-1}\), 17.5 and 11.4 offspring, and 34.0 and 35.0 days, respectively. However, for the cucumbers kept in the field without leaves, the population parameters (\(r, R_0\) and \(T\)) were 0.1043 and 0.0904 day\(^{-1}\), 27.7 and 10.1 offspring, and 32.8 and 27.2 days, respectively. The maximum intrinsic rate of increase (0.1354 d\(^{-1}\)) was obtained at 25°C in the laboratory. All parameters have very high values of CV.

The age-stage specific life expectancy (\(e_{xj}\)) (Fig. 3) is the lifespan remaining for an individual of age \(x\) and stage \(j\). The contribution of an individual of age \(x\) and stage \(j\) to the future population is described by the age-stage reproductive value (\(v_{xj}\)) (Fig. 4). The reproductive value of a newborn (\(v_{01}\)) is exactly equal to the finite rate of increase.

Discussion

Life Table of *B. cucurbitae*

The shorter preadult stage in the treatment under field conditions with leaf
coverage might be due to the higher temperature and the higher humidity. These conditions can promote the decay of cucumber and thereby generate conditions favorable for flies. Vayssières et al. (2008) reported that the total preadult development time of *B. cucurbitae* on cucumber at 25 and 30°C was 17.2 and 13.2 days, respectively. Huang & Chi (2011) reported that the total preadult development time of *B. cucurbitae* was 15.1 days at 25°C. These studies show that the preadult development time of *B. cucurbitae* decreases as the temperature increases. Under field conditions, melon flies in different fallen fruits may experience different micro-environments and may result in higher variations in developmental rate, survival and reproduction.

Because the variable developmental rate among individuals is incorporated in the age-stage, two-sex life table, the overlap between stages can be observed in Fig. 1. If the survival curves were constructed based on the means of each stage or adult age (e.g., Marcic, 2003, 2005; Legaspi, 2004; Legaspi & Legaspi, 2005; Lin & Ren, 2005; Liu, 2005; Kivan & Kilic, 2006; Kontodimas & Stathas, 2005; Tsoukanas et al., 2006), the stage overlap would not have been observed and would have resulted in errors in the survival curves as well as the fecundity curves. Liu (2005) noticed the overlap of the stages of *Delphastus catalinae* (Coleoptera: Coccinellidae). Nevertheless, he ignored the variable developmental rate and constructed age-specific fecundity schedules based on adult age. Yu et al. (2005) and Chi & Su (2006) gave detailed explanations and a mathematical proof to address the errors in life tables based on adult age.

In Vargas et al. (1997), the fecundity of *B. cucurbitae* at 24°C was 578.6 eggs. In Huang & Chi (2011), the mean fecundity of melon flies reared on cucumber at 25°C was 341 eggs. Jiang et al. (2006) reported that the mean fecundity of melon
flies reared on cucumber at 30ºC was 895.65 eggs. In this study, the mean
fecundity of B. cucurbitae reared on whole cucumber at 25ºC was higher than the
fecundity given in Huang & Chi (2011). If the survival rate and fecundity are
constructed based solely on the adult age, the differences in preadult development are
ignored, and it is assumed that all adults emerge on the same day. These artificial
manipulations and assumptions will not only falsely diminish the real variability
among individuals, but also consequently result in errors in the survival and
fecundity curves (Chi, 1988; Yu et al., 2005; Chi & Su, 2006; Huang & Chi, 2011).

Population Parameters

Due to the problems associated with the female age-specific life table (Huang &
Chi, 2011), we used the age-stage, two-sex life table to calculate the population
parameters of B. cucurbitae. The intrinsic rate of increase ($r$) ranged from 0.0904
to 0.1354 days$^{-1}$. The treatments did not differ significantly based on the estimated
means and standard errors obtained by using the jackknife technique and
Tukey-Kramer procedure. The net reproductive rate ($R_0$) of melon flies reared in
the laboratory at 25ºC was higher than the corresponding rate under field conditions.
The relationship between the net reproductive rate $R_0$ and the mean female
fecundity $F$ was given by Chi (1988) for the two-sex life table as

\[ R_0 = F \cdot \left( \frac{N_f}{N} \right) \]  

(2)

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 emerged. Yu et al. (2005) gave the relationship
among the gross reproductive rate ($GRR$), the net reproductive rate ($R_0$) and the
preadult survivorship ($l_a$) as

\[ GRR > l_a \cdot GRR > R_0 \]  

(3)
All of our results for *B. cucurbitae* at different treatments are consistent with the relationships given by equations 2 and 3. If a life table is constructed based on adult age and ignores the preadult mortality, an erroneous relationship between the mean fecundity and the net reproductive rate will be obtained. Yu *et al.* (2005) and Chi & Su (2006) discussed this problem in detail.

The shorter preoviposition period will cause a higher intrinsic rate of increase if fecundity remains the same (Lewontin, 1965). In the study of Huang & Chi (2011), the TPOP of *B. cucurbitae* reared on cucumber at 25°C was 23.1 d. In our study, the TPOP, i.e., the duration from egg to first oviposition, of melon flies reared in the laboratory at 25°C was longer than that under field conditions. This result might be explained by the higher field temperature (28°C) and humidity. At 25°C, the age-stage life expectancy gradually decreases with age because no other adverse effects occur in the laboratory. Under field conditions, however, the life expectancies were lower and varied significantly due to the variable abiotic factors.

The life expectancy is calculated using the age-stage specific survival rate \( s(x,y) \) without assuming that the population reaches the stable age-stage distribution (Chi & Su, 2006). Thus, it can be used to predict the survival of a population under those conditions. For example, at 25°C both newly emerged female and male adults can be expected to remain alive, on average, more than two months. The life expectancy based on the age-stage, two-sex life table reveals the difference among individuals of the same age but of different stages or different sexes. Chi (1988), Chi & Yang (2003) and Chi & Su (2006) discussed in detail the differences between the traditional female age-specific life table and the age-stage, two-sex life table and identified possible errors in the survival and fecundity curves based on the adult age.

Fisher (1930) defined the reproductive value as the contribution of an individual
to the future population. The reproductive value significantly increases at the time of emergence of the adult females. For example, when a female adult emerges at age 15 d at 25°C (Fig. 1), the reproductive value increases from a value of less than 10 for a nymph to 36 for a female (Fig. 4). The contribution of males to the future population is not defined by Fisher (1930), and there is no curve for males.

The research reported here demonstrates that only life table study can completely depict the development, stage differentiation, and reproduction of *B. cucurbitae* and the variability of these processes in whole cucumber. Moreover, it revealed significant differences between life tables collected in the laboratory and the field. Thus, computer simulations of the growth of field populations should incorporate considerations of these differences. Chi (1990) noted that a simulation based on the age-stage, two-sex life table can be used to time pest management by taking the stage-specific susceptibility to pesticide applications into consideration. Chi & Getz (1988) constructed a mass-rearing model based on the age-stage, two-sex life table. For an ecology-oriented integrated pest management of *B. cucurbitae*, life tables collected under different conditions should play important roles in the future. However, because a variety of wild cucurbits serve as a host for the melon fly and form a reservoir for this fly (Uchida *et al.*, 1990), it might be necessary to understand the life table of the fly on the major wild cucurbits.

**Using the Jackknife Method to Estimate of the Net Reproductive Rate**

Our results showed high values of CV in female mean fecundity and population parameters. The high CV in mean fecundity is calculated by using basic descriptive statistical method and they reflect the differences among female individuals. The high CVs of population parameters are, however, estimated by using the jackknife
technique. The jackknife technique is a resampling method which is usually used when replication is impossible or difficult. Because life table studies are time- and labor-consuming, replication is in general impractical in most cases. The jackknife method is thus used to estimate the means and standard errors of population parameters (Chi & Getz, 1988; Maia et al., 2000; Huang & Chi, 2011). In the jackknife method, we first use data on all individuals \( n \) to calculate the intrinsic rate of increase of the whole cohort \( r_{all} \). We then calculate the intrinsic rate \( r_i \) by omitting individual \( i \). The pseudo-value \( r_{i-pseudo} \) is then calculated as:

\[
r_{i-pseudo} = n \cdot r_{all} - (n - 1) r_i
\]

where \( n \) is the total number of individuals used at the beginning of the life table study.

The mean value of all \( r_{i-pseudo} \) is the estimated mean value of the intrinsic rate of increase of the cohort:

\[
r = \frac{\sum_{i=1}^{n} r_{i-pseudo}}{n}
\]

Similarly, if we use the jackknife method to calculate the mean value of the net reproductive rate, we first use data on all individuals in the cohort to calculate \( R_{0,all} \):

\[
R_{0,all} = \sum_{x=0}^{\infty} l_x m_x.
\]

If the total number of eggs laid by all surviving individuals at age \( x \) is \( F_x \), the total eggs laid by the whole cohort from birth to death is \( F_{total} \) and can be calculated as \( \sum_{x=0}^{\infty} F_x \). Then, the \( R_{0,all} \) can also be calculated as

\[
R_{0,all} = \sum_{x=0}^{\infty} l_x m_x = \sum_{x=0}^{\infty} \frac{n_x}{n} \cdot \frac{F_x}{n} = \frac{1}{n} \sum_{x=0}^{\infty} F_x = \frac{F_{total}}{n}
\]

where \( n_x \) is the number of surviving individuals at age \( x \). Equation 7 shows that the net reproductive rate is \( F_{total} \) divided by the total number of individuals \( n \) used at the
beginning of the life table study. If the omitted individual $i$ is type N (those dying at immature stages) or M (male), we define the total eggs laid by $n-1$ individuals at age $x$ as $F_{x,i}$. It is clear that $F_{x,i} = F_x$ for all ages, because types N and M do not lay eggs.

The net reproductive rate with individual $i$ omitted, i.e., $R_{0,i}$, can be calculated as

$$R_{0,i} = \sum_{x=0}^{\infty} \frac{n_{x,i}}{n-1} \frac{F_{x,i}}{n_{x,i}} = \sum_{x=0}^{\infty} \frac{F_{x,i}}{n-1} = \frac{1}{n-1} \sum_{x=0}^{\infty} F_x$$  \hspace{1cm} (8)

where $n_{x,i}$ is the number of surviving individuals at age $x$ if individual $i$ is omitted.

The pseudo-value for the omission of individual $i$ is calculated analogously to Equation 4:

$$R_{0,i-pseudo} = n \cdot R_{0,all} - (n-1) \cdot R_{0,i}$$  \hspace{1cm} (9)

Replacing $R_{0,i}$ according to the proofs of Equation 7 and 8, we find

$$R_{0,i-pseudo} = n \left( \frac{1}{n} \sum_{x=0}^{\infty} F_x \right) - (n-1) \left( \frac{1}{n-1} \sum_{x=0}^{\infty} F_x \right)$$  \hspace{1cm} (10)

Consequently, we obtain

$$R_{0,i-pseudo} = \sum_{x=0}^{\infty} F_x - \sum_{x=0}^{\infty} F_x = 0$$  \hspace{1cm} (11)

Thus, we prove that if the omitted individual $i$ is type N or M, the pseudo-value $R_{0,i-pseudo}$ will always be zero.

If the omitted individual $i$ is a female and can produce $b_{x,i}$ eggs at age $x$, the total number of eggs laid by this female during its life span can be calculated as

$$B_i = \sum_{x=0}^{\infty} b_{x,i}$$  \hspace{1cm} (12)

If individual $i$ is omitted, then the total eggs produced by the remaining individuals in cohort at age $x$ is $F_{x,i}$. It is clear that

$$F_{x,i} = F_x - b_{x,i} \hspace{1cm} \text{or} \hspace{1cm} F_x = F_{x,i} + b_{x,i}$$  \hspace{1cm} (13)

According to Equation 8, we have
\[ R_{0,i} = \frac{1}{n-1} \sum_{x=0}^{\infty} F_{x,i} = \frac{1}{n-1} \sum_{x=0}^{\infty} (F_x - b_{x,i}) \] (14)

The pseudo-value for the omission of individual \( i \) is

\[ R_{0,i-pseudo} = n \cdot R_{0,all} - (n-1) \cdot R_{0,i} \] (15)

Replacing \( R_{0,i} \) of Equation 15 with its value in Equation 14, we can simplify Equation 15 to 16.

\[ R_{0,i-pseudo} = n \left( \frac{1}{n} \sum_{x=0}^{\infty} F_x \right) - (n-1) \left[ \frac{1}{n-1} \sum_{x=0}^{\infty} (F_x - b_{x,i}) \right] \]

\[ R_{0,i-pseudo} = \sum_{x=0}^{\infty} F_x - \sum_{x=0}^{\infty} F_x + \sum_{x=0}^{\infty} b_{x,i} = \sum_{x=0}^{\infty} b_{x,i} = B_i \] (16)

It is clear that if the omitted individual \( i \) is a female, the pseudo-value of the net reproductive rate is exactly the total fecundity of individual \( i \) itself,

\[ R_{0,i-pseudo} = \sum_{x=0}^{\infty} b_{x,i} = B_i \] (17)

This analysis shows that if the jackknife method is used, the pseudo-value of the net reproductive rate obtained by omitting individual \( i \) is exactly the total number of eggs laid by individual \( i \). It is exactly the fecundity of individual \( i \). The mean of all pseudo-values is the total number of eggs laid by all individuals divided by \( n \):

\[ \hat{R}_0 = \frac{\sum_{i=1}^{n} R_{0,i-pseudo}}{n} = \frac{\sum_{i=1}^{n} B_i}{n} \] (18)

By definition, it is clear that \( \sum_{i=1}^{n} B_i = \sum_{x=0}^{\infty} F_x \).

The mean of all \( R_{0,i-pseudo} \) is then

\[ \hat{R}_0 = \frac{\sum_{i=1}^{n} B_i}{n} = \frac{\sum_{x=0}^{\infty} F}{n} = R_{0,all} \]. (19)

The above proof can be concluded by making the following four observations: 1)
the mean value of the net reproductive rate estimated with the jackknife method is

exactly the same as the $R_{0,all}$ without the use of the jackknife method; 2) the net

reproductive rate equals the total eggs of the cohort divided by $n$, i.e., the total

number of newborns used for the life table study; 3) if the omitted individual is one

of the males or one of those that died at an immature stage, the pseudo-value is zero;

and 4) if the omitted individual is female, the pseudo-value is the fecundity of that

omitted female.

In Fig. 5, the frequency distributions of pseudo-$R_0$ values of three treatments

showed the zeros obtained by using the jackknife technique. It is clear that the

omission of a single individual of type N or M will generate a pseudo-$R_0$ of zero.

The higher the preadult mortality or proportion of male, the higher the zero

pseudo-$R_0$ bar. Because there is generally preadult mortality, the bar of zero

pseudo-$R_0$ will be an important factor determining the frequency distribution of all

life table data. This is also the reason why statistical software shows the pseudo-$R_0$

failed the normality test and instead suggests Mann-Whitney Rank Sum test or others.

The omission of a single individual of type N or M caused the pseudo-$R_0$ of the

resampled population to zero. If we carry out a true replication of life table study as

we did in this study, however, we will generally not get a population with zero net

reproductive rate, i.e., all individuals are either type N or M. This shows the

jackknife technique will generate biologically unrealistic pseudo-$R_0$, which results in

an overestimation of variances and standard errors of the net reproductive rates.

The overestimation of variances and standard errors consequently make significant

differences between treatments undetectable by using statistical tests.

Variance analysis is important for revealing the variability of experimental

results. The question of the suitability of the jackknife method for the estimation of
the mean and standard errors of the net reproductive rate is not the only difficulty
associated with life table analysis. The sample size must be sufficiently large to
prevent inaccurate estimation of the standard errors. Because there are many
problems associated with female life tables and analyses based on adult age (Chi &
Liu, 1985; Chi, 1988; Yu et al., 2005; Chi & Su, 2006; Huang & Chi, 2011), the
application of the jackknife method to female life tables (Leslie, 1945; Birch, 1948;
Maia et al., 2000) or in analyses based on female population and adult age (Maia et
al., 2000) will not produce correct estimates.

The significant differences between replicates in this study showed, however,
that the variability in developmental rate, survival, and reproduction of a life table
could not be properly described and estimated with the jackknife method. For this
reason and many others, the prediction of population dynamics under field conditions
is difficult. In this paper, we limit our discussion to the application of jackknife
method to the net reproductive rate. There are other resampling methods, e.g.,
bootstrapping, permutation test, cross validation, etc. Similar analysis is required to
re-evaluate their application in the estimation of means and variances of population
parameters. Despite these difficulties and problems, the life table is the only solid
theory which can correctly describe the survival, stage differentiation, and
reproduction in detail. The necessity and the difficulties associated with life table
study demonstrate that we need to draw the attention of scientists to life table theory
and data analysis in insect ecology, integrated pest management, as well as biological
control.
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References


Table 1. Means and standard errors of the developmental time, longevity, adult preoviposition period (APOP) and total preoviposition period (TPOP) of *Bactrocera cucurbitae* for different treatments

<table>
<thead>
<tr>
<th>Parameter</th>
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<th>Field conditions</th>
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<td>Rep. 1</td>
<td>Rep. 2</td>
<td>Rep. 1</td>
<td>Rep. 2</td>
</tr>
<tr>
<td>Developmental time</td>
<td>Preadult</td>
<td>17.8 ± 0.2 a</td>
<td>18.5 ± 0.2 b</td>
<td>11.4 ± 0.2 c</td>
<td>11.4 ± 0.1 c</td>
</tr>
<tr>
<td>time (days)</td>
<td>Male</td>
<td>74.8 ± 7.1 a</td>
<td>63.2 ± 9.5 a</td>
<td>33.6 ± 13.1 b</td>
<td>34.7 ± 11.8 b</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>58.9 ± 6.5 a</td>
<td>45.6 ± 12.0 a</td>
<td>55.4 ± 11.6 a</td>
<td>16.3 ± 4.7 b</td>
</tr>
<tr>
<td>Adult longevity</td>
<td>Male</td>
<td>74.8 ± 7.1 a</td>
<td>63.2 ± 9.5 a</td>
<td>33.6 ± 13.1 b</td>
<td>34.7 ± 11.8 b</td>
</tr>
<tr>
<td>(days)</td>
<td>Female</td>
<td>58.9 ± 6.5 a</td>
<td>45.6 ± 12.0 a</td>
<td>55.4 ± 11.6 a</td>
<td>16.3 ± 4.7 b</td>
</tr>
<tr>
<td>APOP (days)</td>
<td>Female</td>
<td>8.7 ± 0.3 a</td>
<td>8.9 ± 0.6 a</td>
<td>9.1 ± 0.3 a</td>
<td>8.6 ± 0.4 a</td>
</tr>
<tr>
<td>TPOP (days)</td>
<td>Female</td>
<td>26.7 ± 0.3 a</td>
<td>28.0 ± 0.8 b</td>
<td>20.7 ± 0.3 c</td>
<td>20.0 ± 0.3 c</td>
</tr>
</tbody>
</table>

Means in the same row followed by the same letter are not significantly different (*P* > 0.05) using the Tukey-Kramer procedure.
Table 2. Means, standard errors, and coefficients of variation (CV) (in parentheses) of the population parameters of *Bactrocera cucurbitae* for different treatments

<table>
<thead>
<tr>
<th>Population parameters</th>
<th>25°C</th>
<th>Field conditions</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean fecundity ((F)) (eggs/female)</td>
<td>859.5 ± 107.8 a (61.4%)</td>
<td>660.1 ± 179.9 a (86.2%)</td>
<td>345.9 ± 92.5 b (75.6%)</td>
<td>112.1 ± 42.8 b (114.4%)</td>
</tr>
<tr>
<td>The intrinsic rate of increase (r) (days(^{-1}))</td>
<td>0.1354 ± 0.0060 a (44.0%)</td>
<td>0.1002 ± 0.0116 a (116.2%)</td>
<td>0.1043 ± 0.0151 a (145.2%)</td>
<td>0.0904 ± 0.0197 a (217.3%)</td>
</tr>
<tr>
<td>The finite rate of increase (\lambda) (days(^{-1}))</td>
<td>1.145 ± 0.007 a (6%)</td>
<td>1.105 ± 0.013 a (11.6%)</td>
<td>1.110 ± 0.017 a (15.1%)</td>
<td>1.094 ± 0.021 a (19.5%)</td>
</tr>
<tr>
<td>Gross reproductive rate ((GRR)) (offspring)</td>
<td>636.3 ± 129.6 a (203.6%)</td>
<td>426.5 ± 159.5 a (374.6%)</td>
<td>322.4 ± 120.0 a (372.1%)</td>
<td>119.3 ± 56.4 a (473.0%)</td>
</tr>
<tr>
<td>The net reproductive rate (R_0) (offspring/individual)</td>
<td>206.3 ± 44.8 a (217.3%)</td>
<td>66.0 ± 26.3 b (398.0%)</td>
<td>27.7 ± 11.7 b (423.5%)</td>
<td>10.1 ± 4.9 b (482.4%)</td>
</tr>
<tr>
<td>The mean generation time (T) (days)</td>
<td>39.5 ± 0.8 a (19.1%)</td>
<td>42.6 ± 1.5 a (34.3%)</td>
<td>32.8 ± 1.5 a (45.7%)</td>
<td>27.2 ± 2.3 b (83.2%)</td>
</tr>
</tbody>
</table>

Means in the same row followed by the same letter are not significantly different \((P > 0.05)\) using the Tukey-Kramer procedure.
Figure captions

Fig. 1. Age-stage specific survival rate \( (s_{ij}) \) of \textit{Bactrocera cucurbitae} for different treatments.

Fig. 2. Age-specific survival rate \( (l_x) \), female age-specific fecundity \( (f_{x2}) \), age-specific fecundity \( (m_x) \) and age-specific maternity \( (l_xm_x) \) of \textit{Bactrocera cucurbitae} for different treatments.

Fig. 3. Age-stage specific life expectancy \( (e_{ij}) \) of \textit{Bactrocera cucurbitae} for different treatments.

Fig. 4. Age-stage specific reproductive value \( (v_{ij}) \) of \textit{Bactrocera cucurbitae} for different treatments.

Fig. 5. Frequency distribution of pseudo-\( R_0 \) grouped for different treatments. Each bar represents the number of pseudo-\( R_0 \) between two ticks. The bar at zero represents the frequency of pseudo-\( R_0 \) zero.
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