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ORIGINAL CONTRIBUTION

Life tables of *Bactrocera cucurbitae* (Diptera: Tephritidae): with an invalidation of the jackknife technique

Y.-B. Huang & H. Chi

Laboratory of Theoretical and Applied Ecology, Department of Entomology, National Chung Hsing University Taichung, Taiwan, Republic of China

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Correspondence
Hsin Chi (corresponding author), P.O. Box 17-25, Taichung, Taiwan, Republic of China. E-mail: hsinchi@dragon.nchu.edu.tw

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Abstract

Life table gives the most comprehensive description on the survival, stage differentiation and reproduction of a population and is thus the most important basis of population ecology and pest management. In this study, we constructed life tables for *Bactrocera cucurbitae* on cucumber (*Cucumis sativus* L.) in the laboratory and under simulated field conditions. To assess the variability of the life tables, we carried out two experiments under each treatment. Means, variances and standard errors of life table parameters were estimated for each of the two experiments by using the jackknife technique. At 25°C, the intrinsic rates of increase (r) found for the two experiments were 0.1354 and 0.1002 per day, and the net reproductive rates (R_0) were 206.3 and 66.0 offspring, respectively. For cucumbers kept in the field and covered with leaves, the r and R_0 for the two experiments were 0.0935 and 0.0909 per day, and 17.5 and 11.4 offspring, respectively. However, if cucumbers were kept in the field but were not covered, the r and R_0 for the two experiments were 0.1043 and 0.0904 per day, and 27.7 and 10.1 offspring, respectively. Our results revealed significant variability between the experiments under both laboratory and field conditions; this variability should be taken into consideration in the data collection and application of life tables. However, our mathematical analysis shows that the application of the jackknife technique will result in biologically unrealistic $R_{0,i\text{-pseudo}}$ and consequently overestimation of the variance of R_0. According to our analysis, we suggest that the jackknife technique should not be used for the estimation of variability of the net reproductive rate.

Introduction

The melon fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), has been one of the most important pests in Taiwan (Huang and Chi 2012) 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 and Chi 2012). 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 programmes because only life tables can provide the most detailed and correct descriptions of the survival, stage differentiation and reproduction of populations. Female age-specific 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 and 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 and Chi (2012) 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 a female age-specific 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 the 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, because of the tedious and time-consuming work of life table studies, most life table studies are carried out by using a 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 and Tibshirani (1993) discussed the failure of jackknife. Chi and 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 $R_{0,i\text{-pseudo}}$ value of zero. A 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 (*Cucumis sativus* L.). The cucumbers were then kept in the laboratory at 25°C or under placed in the field and exposed to field conditions. Survival rate and fecundity of emerged adults were used to construct life tables. To assess the variability of the life table study, two experiments were carried out under each treatment. Life tables were constructed and the population parameters were measured for each of the experiments. Furthermore, we derived a mathematical proof to demonstrate the problems that occur when the jackknife method is used for the estimation of the mean and variance of the net reproductive rate.

Materials and Methods

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 and Chi (2012). 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 29 September 2006. The average field temperature was 28.1°C. Two experiments were carried out 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 the study by Huang and Chi (2012).

Demographic analysis

The life history data were analysed according to the age-stage, two-sex life table theory (Chi and Liu 1985) and the method described by Chi (1988). The population parameters estimated were the intrinsic rate of increase (r), the finite rate of increase (λ), the gross reproductive rate (GRR), the net reproductive rate (R_0) and the mean generation time (T). In this study, the intrinsic rate of increase is estimated using the iterative bisection method from the Euler–Lotka

formula:

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

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. $e^{rT} = R_0$ 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 and Su (2006). The means, variances and standard errors of the life table parameters were estimated with the jackknife method (Sokal and Rohlf 1995). 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/wes/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 and Rohlf (1995).

Results

Life table of *Bactrocera cucurbitae*

The developmental times for each stage are listed in table 1. At 25°C, the duration of the pre-adult stage in a whole cucumber was 17.8 and 18.5 days for the two experiments, respectively. 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 in the different treatments ranged from 7.0 to 9.1 days. 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_{xj}) of *B. cucurbitae* for the different treatments are plotted in fig. 1. The parameter s_{xj} 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 experiments 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 pre-adult 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_{xj}) in fig. 2. Because only adult females produce offspring, there is only a single curve f_{x2} (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 experiments. In one experiment at 25°C, more than 40% *B. cucurbitae* survived to the adult stage, but the corresponding value in another experiment was much smaller, approximately 20%. However, at 25°C, the survival

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

				Field conditions			
		25°C		Without leaf coverage		With leaf coverage	
Parameter	Stage	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2
Developmental time (days)	Preadult	17.8 ± 0.2 a	18.5 ± 0.2 b	11.4 ± 0.2 c	11.4 ± 0.1 c	11.0 ± 0.0 c	11.2 ± 0.2 c
Adult longevity (days)	Male	74.8 ± 7.1 a	63.2 ± 9.5 a	33.6 ± 13.1 b	34.7 ± 11.8 b	63.9 ± 9.8 a	13.2 ± 8.7 b
	Female	58.9 ± 6.5 a	45.6 ± 12.0 a	55.4 ± 11.6 a	16.3 ± 4.7 b	28.5 ± 8.9 a	22.6 ± 14.5 a
APOP (days)	Female	8.7 ± 0.3 a	8.9 ± 0.6 a	9.1 ± 0.3 a	8.6 ± 0.4 a	9.0 ± 0.6 a	7.0 ± 2.0 a
TPOP (days)	Female	26.7 ± 0.3 a	28.0 ± 0.8 b	20.7 ± 0.3 c	20.0 ± 0.3 c	20.0 ± 0.6 c	18.5 ± 1.5 c

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 (CV is calculated as standard deviation/mean)

			Field conditions			
	25°C		Without leaf coverage		With leaf coverage	
Population parameters	Experiment 1	Experiment 2	Experiment 1	Experiment 2	Experiment 1	Experiment 2
Mean fecundity (*F*) (eggs/female)	859.5 ± 107.8 a (61.4%)	660.1 ± 179.9 a (86.2%)	345.9 ± 92.5 b (75.6%)	112.1 ± 42.8 b (114.4%)	218.5 ± 115.5 b (149.5%)	227.6 ± 162.3 b (159.5%)
The intrinsic rate of increase *r* (per days)	0.1354 ± 0.0060 a (44.0%)	0.1002 ± 0.0116 a (116.2%)	0.1043 ± 0.0151 a (145.2%)	0.0904 ± 0.0197 a (217.3%)	0.0935 ± 0.0120 a (224.3%)	0.0909 ± 0.0380 a (417.3%)
The finite rate of increase λ (per days)	1.145 ± 0.007 a (6%)	1.105 ± 0.013 a (11.6%)	1.110 ± 0.017 a (15.1%)	1.094 ± 0.021 a (19.5%)	1.098 ± 0.023 a (20.7%)	1.094 ± 0.040 a (36.9%)
Gross reproductive rate (*GRR*) (offspring)	636.3 ± 129.6 a (203.6%)	426.5 ± 159.5 a (374.6%)	322.4 ± 120.0 a (372.1%)	119.3 ± 56.4 a (473.0%)	146.5 ± 94.7 a (646.3%)	868.61 ± 484.84 a (558.2%)
The net reproductive rate R_0 (offspring/individual)	206.3 ± 44.8 a (217.3%)	66.0 ± 26.3 b (398.0%)	27.7 ± 11.7 b (423.5%)	10.1 ± 4.9 b (482.4%)	17.5 ± 10.5 b (602.5%)	11.4 ± 8.8 b (776.4%)
The mean generation time *T* (days)	39.5 ± 0.8 a (19.1%)	42.6 ± 1.5 a (34.3%)	32.8 ± 1.5 a (46.7%)	27.2 ± 2.3 b (83.2%)	34.0 ± 3.9 a (113.4%)	35.0 ± 7.4 a (212.2%)

Means in the same row followed by the same letter are not significantly different ($P > 0.05$) using the Tukey–Kramer procedure.

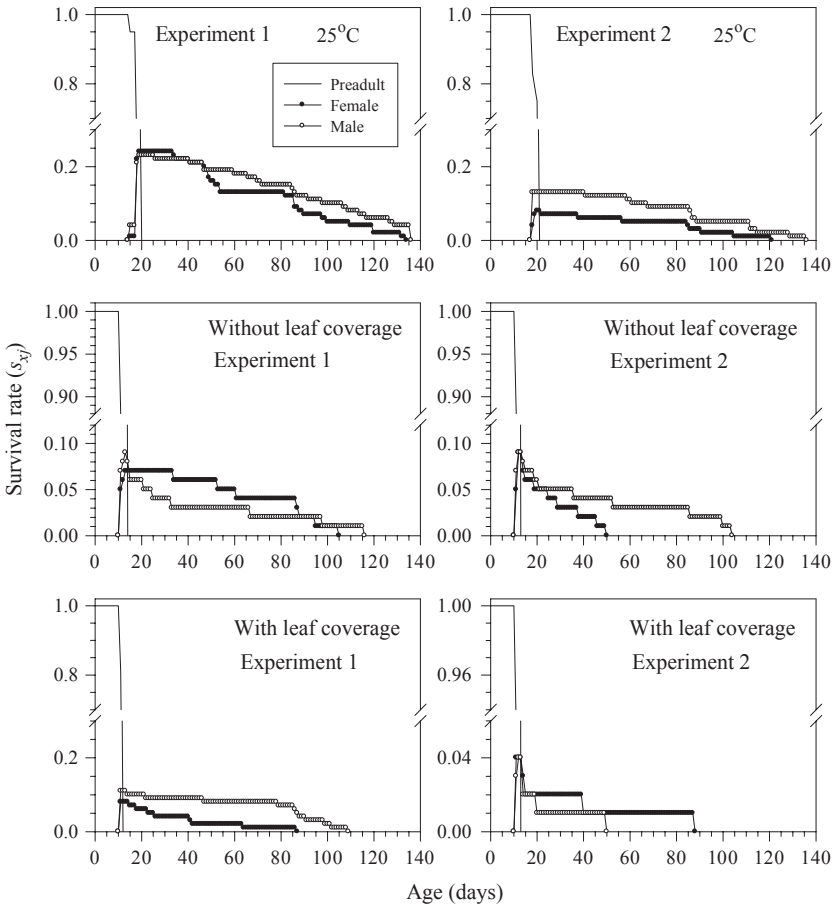

Fig. 1 Age-stage-specific survival rate (s_{xj}) of *Bactrocera cucurbitae* for different treatments.

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 experiments were 0.1354 and 0.1002 per day, 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 per day, 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 per day, 27.7 and 10.1 offspring and 32.8 and 27.2 days, respectively. The maximum intrinsic rate of increase (0.1354 per day) 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 *Bactrocera cucurbitae*

The shorter pre-adult 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 favourable for flies. Vayssières et al. (2008) reported that the total pre-adult development time of *B. cucurbitae* on cucumber at 25 and 30°C was 17.2 and 13.2 days, respectively.

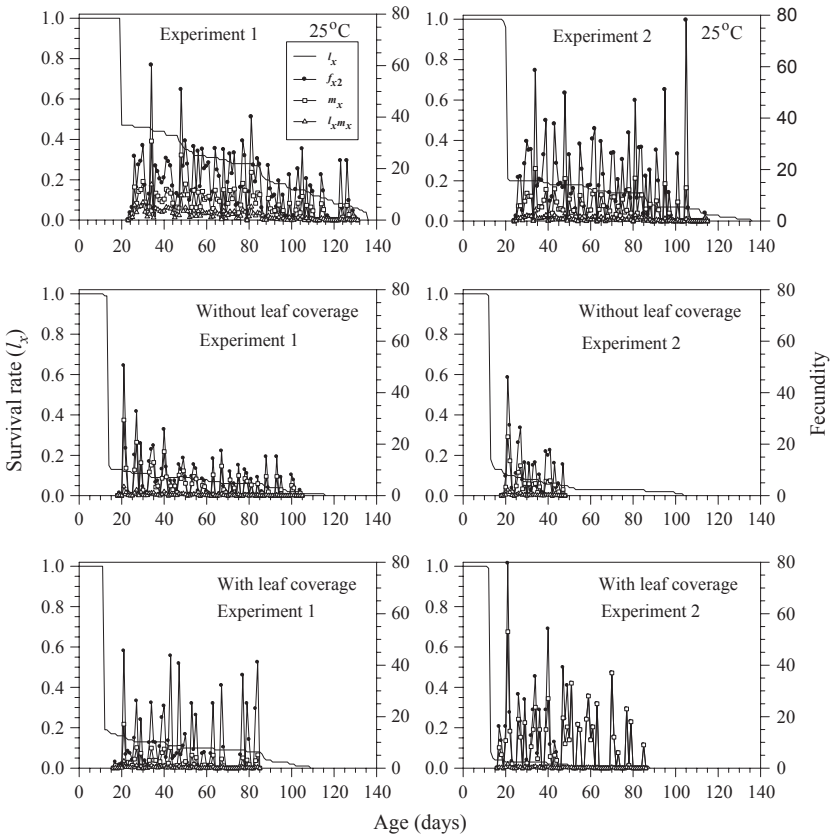

Fig. 2 Age-specific survival rate (l_x), female age-specific fecundity (f_{x2}), age-specific fecundity (m_x) and age-specific maternity ($l_x m_x$) of *Bactrocera cucurbitae* for different treatments.

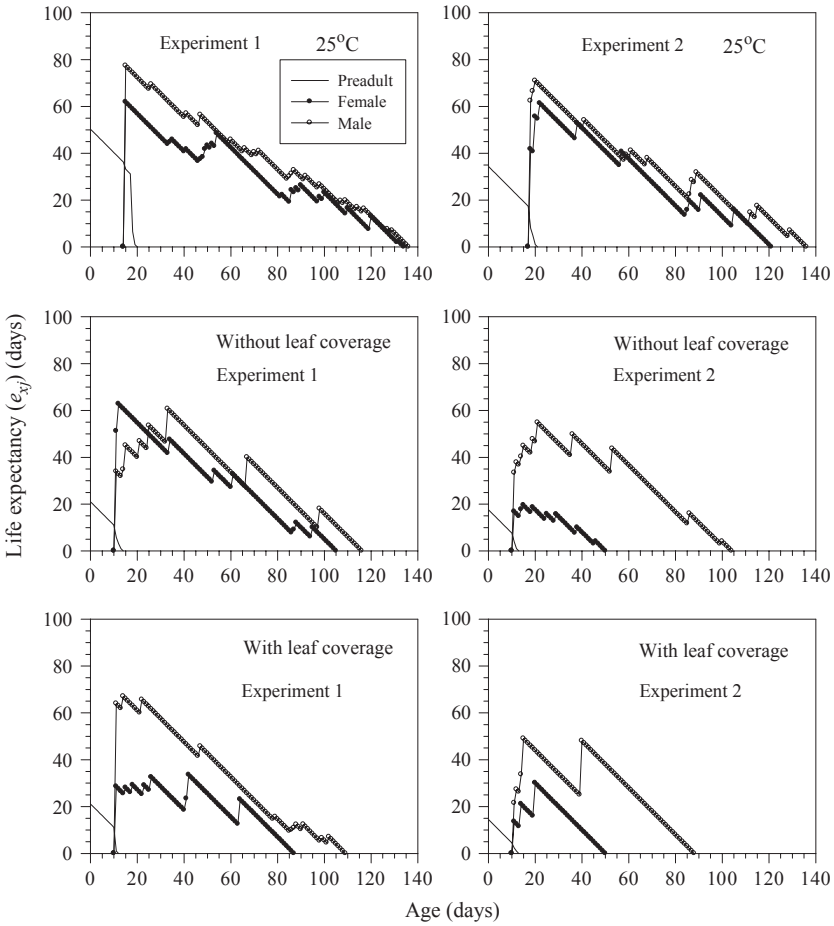

Fig. 3 Age-stage-specific life expectancy (e_{xj}) of *Bactrocera cucurbitae* for different treatments.

Huang and Chi (2012) reported that the total pre-adult development time of *B. cucurbitae* was 15.1 days at 25°C. These studies show that the pre-adult development time of *B. cucurbitae* decreases as the temperature increases. Under field conditions, melon flies in different fallen fruits may experience different microenvironments 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; Kontodimas and Stathas 2005; Legaspi and Legaspi 2005; Lin and Ren 2005; Liu 2005; Kivan and Kilic 2006; 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 and Su (2006) gave detailed explanations and a mathematical proof to address the errors in life tables based on adult age.

In the study by Vargas et al. (1997), the fecundity of *B. cucurbitae* at 24°C was 578.6 eggs. In the study by Huang and Chi (2012), 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 30°C was 895.65 eggs. In this study, the mean fecundity of *B. cucurbitae* reared on whole cucumber at 25°C was higher than the fecundity given in the study by Huang and Chi (2012). If the survival rate and fecundity are constructed based solely on the adult age, the differences in pre-adult 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

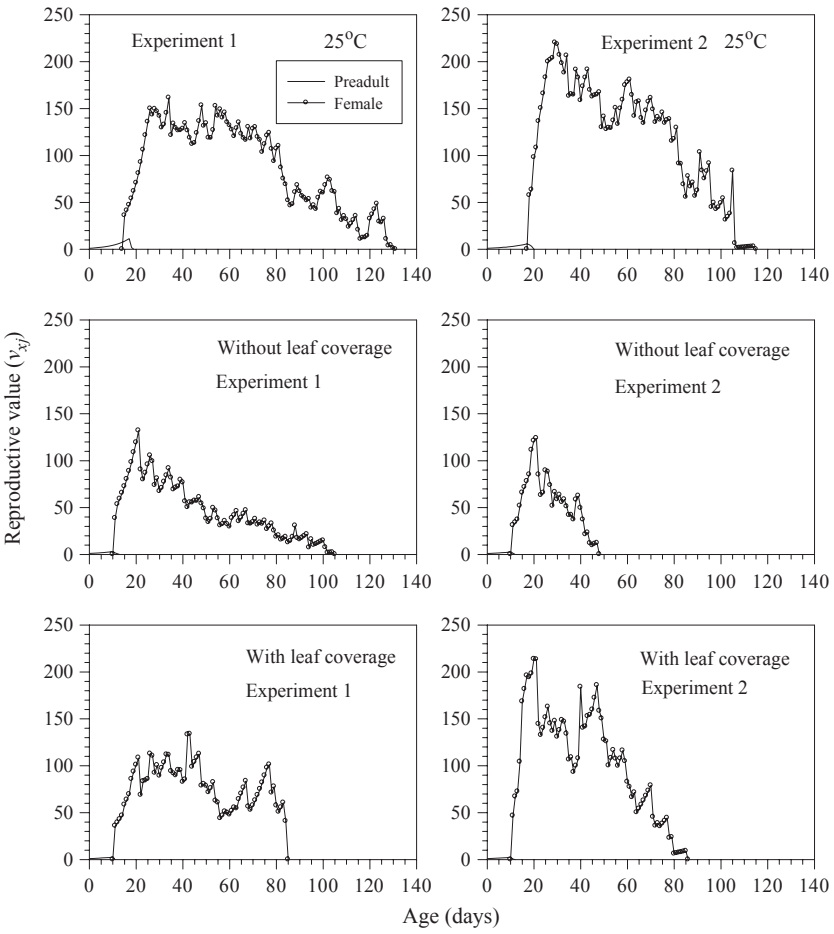

Fig. 4 Age-stage-specific reproductive value (v_{xj}) of *Bactrocera cucurbitae* for different treatments.

result in errors in the survival and fecundity curves (Chi 1988; Yu et al. 2005; Chi and Su 2006; Huang and Chi 2012).

Population parameters

Because of the problems associated with the female age-specific life table (Huang and Chi 2012), 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 per days. 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 25°C 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

$$R_0 = F \cdot \left(\frac{N_f}{N}\right) \tag{2}$$

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 *GRR*, the net reproductive rate (R_0) and the pre-adult survivorship (l_a) as

$$GRR > l_a \cdot GRR > R_0 \tag{3}$$

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

The shorter pre-oviposition period will cause a higher intrinsic rate of increase if fecundity remains

the same (Lewontin 1965). In the study of Huang and Chi (2012), the TPOP of *B. cucurbitae* reared on cucumber at 25°C was 23.1 days. In our study, the TPOP, that is, 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 because of the variable abiotic factors. The life expectancy is calculated using the age-stage-specific survival rate (s_{xj}) without assuming that the population reaches the stable age-stage distribution (Chi and 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, for more than 2 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 and Yang (2003) and Chi and 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 days at 25°C, the reproductive value increases from a value of <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 a whole cucumber. Moreover, it revealed significant differences between life tables collected in the laboratory and in 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 and 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 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 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 the 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 labour-consuming, replication is in general impractical in most cases. The jackknife method is thus used to estimate the means, variances and standard errors of population parameters (Chi and Getz 1988; Maia et al. 2000; Huang and Chi 2012). 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 $r_{i\text{-pseudo}}$ is then calculated as

$$r_{i-\text{pseudo}} = n \cdot r_{\text{all}} - (n-1)r_i \tag{4}$$

where n is the total number of individuals used at the beginning of the life table study. The mean value of all $r_{i\text{-pseudo}}$ is the estimated mean value of the intrinsic rate of increase of the cohort:

$$r = \frac{\sum_{i=1}^{n} r_{i-\text{pseudo}}}{n} \tag{5}$$

Similarly, if we use the jackknife method to calculate the mean value of the net reproductive rate. An example with hypothetical data is given in table 3. We first use data on all individuals in the cohort to calculate $R_{0,\text{all}}$:

$$R_{0,\text{all}} = \sum_{x=0}^{\infty} l_x m_x. \tag{6}$$

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 $R_{0,\text{all}}$ can also be calculated as

Table 3 Example of data analysis using the jackknife technique

		Age-specific survival and fecundity														
		Age (x)											Net reproductive rate		Intrinsic rate of increase	
Ind. no. (i)	Sex	0	1	2	3	4	5	6	7	8	9	10	B_i	$R_{0,i}$	$R_{0,i\text{-pseudo}}$	r_i	$r_{i\text{-pseudo}}$
1	F	I	I	I	I	I	A,0	A,12	7	0	0	d	19	7.89	19	0.2635	0.4776
2	F	I	I	I	I	I	I	A,0	11	7	3	d	21	7.67	21	0.2715	0.4055
3	F	I	I	I	I	A,0	A,14	A,6	A,2	2	d		24	7.33	24	0.2409	0.6806
4	F	I	I	I	I	I	I	I	10	8	8	d	26	7.11	26	0.2667	0.4485
5	M	I	I	I	I	I	A	A	A	A	A	d	–	10	0	0.2990	0.1584
6	M	I	I	I	I	A	A	A	A	d			–	10	0	0.2990	0.1584
7	M	I	I	I	A	A	A	A	A	d			–	10	0	0.2990	0.1584
8	M	I	I	I	I	A	A	A	A	d			–	10	0	0.2990	0.1584
9	N	I	I	I	I	I	d						–	10	0	0.2990	0.1584
10	N	I	I	d									–	10	0	0.2990	0.1584
Population parameters (mean ± SE) estimated by using the jackknife technique: $R_{0,J} = 9 \pm 3.72$, $r_J = 0.2963 \pm 0.0605$																	
l_x		1	1	0.9	0.9	0.9	0.8	0.8	0.8	0.5	0.4	0	$R_{0,\text{all}} = 9$				
m_x		0	0	0	0	0	1.75	2.25	3.75	3.4	2.75	0	$r_{\text{all}} = 0.2849$				
$l_x m_x$		0	0	0	0	0	1.4	1.8	3.0	1.7	1.1	0	Mean fecundity = 22.5 ± 1.6				

F: female, M: male, N: individual died in immature stage. I: immature stage, A: adult, d: death. Number following the symbol A of female is the daily fecundity of female. Age-specific survival rate (l_x), fecundity (m_x), $R_{0,\text{all}}$ and r_{all}: are calculated using all individuals. $R_{0,J}$ and r_J are the estimated means of the net reproductive rate and intrinsic rate of increase calculated using the jackknife technique. B_i is the total number of eggs produced by individual i.

$$R_{0,\text{all}} = \sum_{x=0}^{\infty} l_x m_x = \sum_{x=0}^{\infty} \frac{n_x}{n} \cdot \frac{F_x}{n_x} = \sum_{x=0}^{\infty} \frac{F_x}{n} = \frac{1}{n} \sum_{x=0}^{\infty} F_x = \frac{F_{\text{total}}}{n} \tag{7}$$

where n_x is the number of surviving individuals at age x. Equation 7 shows that the net reproductive rate can also be simply calculated as F_{total} divided by the total number of individuals, n used at the beginning of the life table study. In the jackknife method, we calculate the net reproductive rate with individual i omitted, that is, $R_{0,i}$, as

$$R_{0,i} = \sum_{x=0}^{\infty} l_{x,i} m_{x,i} \tag{8}$$

where $l_{x,i}$ and $m_{x,i}$ are the age-specific survival rate and fecundity of the population minus individual i. 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. Then the net reproductive rate, minus individual i, that is, $R_{0,i}$, can be calculated as

$$R_{0,i} = \sum_{x=0}^{\infty} \frac{n_{x,i}}{n-1} \cdot \frac{F_{x,i}}{n_{x,i}} = \sum_{x=0}^{\infty} \frac{F_{x,i}}{n-1} = \sum_{x=0}^{\infty} \frac{F_x}{n-1} = \frac{1}{n-1} \sum_{x=0}^{\infty} F_x \tag{9}$$

where $n_{x,i}$ is the number of surviving individuals at age x if individual i is omitted. Clearly, eqns 8 and 9 generate the same $R_{0,i}$. The $R_{0,i\text{-pseudo}}$ obtained by omitting individual i is calculated analogously to eqn 4:

$$R_{0,i-\text{pseudo}} = n \cdot R_{0,\text{all}} - (n-1) \cdot R_{0,i}. \tag{10}$$

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

$$R_{0,i-\text{pseudo}} = n\left(\frac{1}{n}\sum_{x=0}^{\infty} F_x\right) - (n-1)\left(\frac{1}{n-1}\sum_{x=0}^{\infty} F_x\right). \tag{11}$$

Consequently, we obtain

$$R_{0,i-\text{pseudo}} = \sum_{x=0}^{\infty} F_x - \sum_{x=0}^{\infty} F_x = 0 \tag{12}$$

Thus, we prove that if the omitted individual i is type N or M, the $R_{0,i\text{-pseudo}}$ 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

$$B_i = \sum_{x=0}^{\infty} b_{x,i}. \tag{13}$$

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

$$F_{x,i} = F_x - b_{x,i} \text{ or } F_x = F_{x,i} + b_{x,i}. \quad (14)$$

According to eqn 9, we have

$$R_{0,i} = \frac{1}{n-1}\sum_{x=0}^{\infty} F_{x,i} = \frac{1}{n-1}\sum_{x=0}^{\infty}\left(F_x - b_{x,i}\right) \quad (15)$$

The $R_{0,i\text{-pseudo}}$ for the omission of individual i is

$$R_{0,i-\text{pseudo}} = n \cdot R_{0,\text{all}} - (n-1) \cdot R_{0,i} \quad (16)$$

Replacing $R_{0,i}$ of eqn 16 with its value in eqn 15, we can simplify eqn 16 to 17.

$$R_{0,i-\text{pseudo}} = n \cdot \left(\frac{1}{n}\sum_{x=0}^{\infty} F_x\right) - (n-1)\left[\frac{1}{n-1}\sum_{x=0}^{\infty}\left(F_x - b_{x,i}\right)\right] \quad (17)$$

$$R_{0,i-\text{pseudo}} = \sum_{x=0}^{\infty} F_x - \sum_{x=0}^{\infty} F_x + \sum_{x=0}^{\infty} b_{x,i} = \sum_{x=0}^{\infty} b_{x,i} = B_i$$

It is clear that if the omitted individual i is a female, the $R_{0,i\text{-pseudo}}$ is exactly the total fecundity of individual i itself:

$$R_{0,i-\text{pseudo}} = \sum_{x=0}^{\infty} b_{x,i} = B_i \quad (18)$$

This analysis shows that if the jackknife method is used, the $R_{0,i\text{-pseudo}}$ obtained by omitting individual i is exactly the total number of eggs laid by the individual i (table 3). Our proof explains that the statement of Armitage et al. (2002, p. 304) 'Indeed, if g is the sample mean, the ith pseudo-values is the ith observation.' is true when the jackknife method is applied to the estimation of the mean of the net reproductive rate. The mean of all $R_{0,i\text{-pseudo}}$ is the total number of eggs laid by all individuals divided by n:

$$\hat{R}_0 = \frac{\sum_{i=1}^{n} R_{0,i-\text{pseudo}}}{n} = \frac{\sum_{i=1}^{n} B_i}{n}. \quad (19)$$

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

The mean of all $R_{0,i\text{-pseudo}}$ is then

$$\hat{R}_0 = \frac{\sum_{i=1}^{n} B_i}{n} = \frac{\sum_{i=0}^{\infty} F}{n} = R_{0,\text{all}}. \quad (20)$$

Because calculating the intrinsic rate of increase (eqn 1) is not a simple problem of 'sample mean', Armitage et al.'s statement 'Indeed, if g is the sample mean, the ith pseudo-values is the ith observation.' is no more valid in the application of jackknife method to the intrinsic rate of increase. As shown in table 3, when the 5th individual is omitted, we obtained a zero for $R_{0,5\text{-pseudo}}$ and a non-zero $r_{5\text{-pseudo}}$ (0.2990). Lotka (1913, p. 293) proved that 'In the first place it can be seen by inspection that $r >= < 0$ according as $\int_0^{\infty} p_m(a)\beta_m(a)da >= < 1$', where $p_m(a)$ and $\beta_m(a)$ are the age-specific survival rate and fecundity, respectively. Using notation consistent with this study, this equation is equivalent to $\sum l_x m_x >= < 1$. Thus, the application of the jackknife method to population parameters (R_0, r, λ, and T) results in inconsistent relationships between the net reproductive rate and intrinsic rate of increase as proven by both Lotka (1913) and Lewis (1942). These zeros are generated by the calculation procedures (eqns 8–10) of the jackknife method. In actual life table studies, however, we will never, realistically, find a population with a zero net reproductive rate, that is, all individuals are either type N or M. Therefore, these zeros are biologically meaningless estimates of the net reproductive rate.

The above proof can be concluded by making the following four observations: (i) the mean value of the net reproductive rate estimated with the jackknife method is exactly the same as the $R_{0,\text{all}}$ without the use of the jackknife method; (ii) the net reproductive rate equals the total eggs of the cohort divided by n, that is, the total number of newborns used for the life table study; (iii) if the omitted individual i is one of the males or one of those that died at an immature stage, the $R_{0,i\text{-pseudo}}$ is zero; and (iv) if the omitted individual is female, the $R_{0,i\text{-pseudo}}$ is the fecundity of that omitted female.

In fig. 5, the frequency distributions of $R_{0,i\text{-pseudo}}$ 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 $R_{0,i\text{-pseudo}}$ of zero. When the pre-adult mortality is high, the high frequency of zero $R_{0,i\text{-pseudo}}$ produces a heavily skewed distribution. This skewness is, however, because of the biologically meaningless zeros in $R_{0,i\text{-pseudo}}$. This is one of the reasons that the jackknife method should not be used. Because there is generally pre-adult mortality, the bar of zero $R_{0,i\text{-pseudo}}$ will be an important factor determining the frequency distribution of all life table data. This is also the reason why statistical software shows the distribution of $R_{0,i\text{-pseudo}}$ 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 $R_{0,i\text{-pseudo}}$ of the resampled population to zero. Because all these

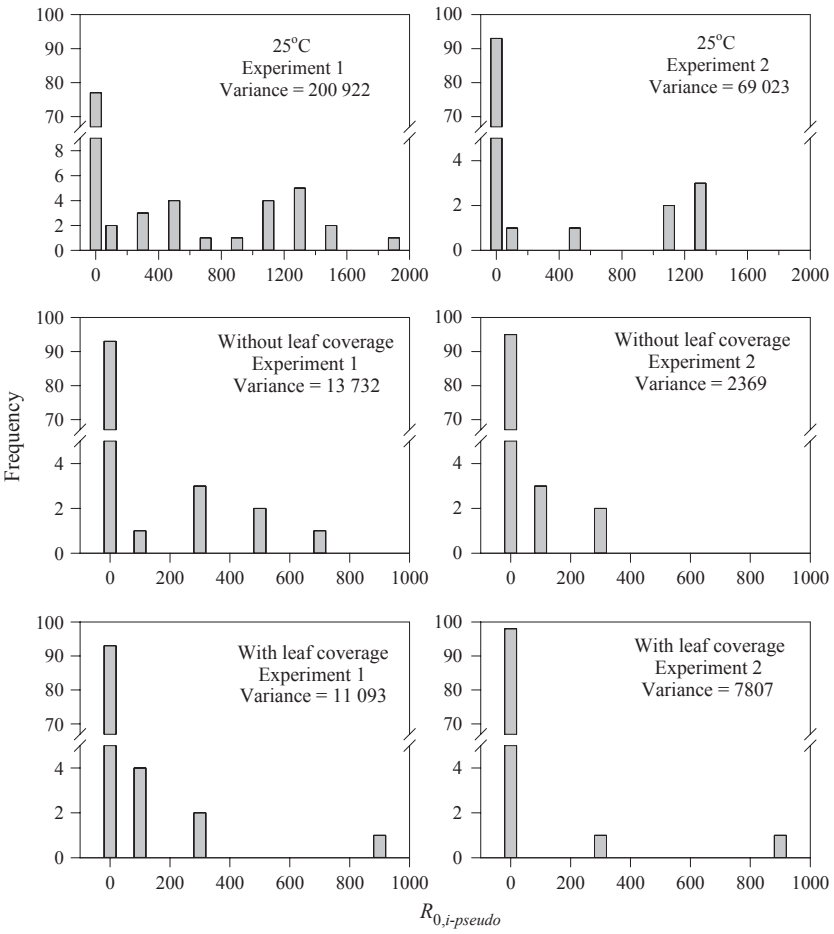

Fig. 5 Frequency distribution of $R_{0,i\text{-pseudo}}$ grouped for different treatments. Each bar represents the number of $R_{0,i\text{-pseudo}}$ between two ticks. The bar at zero represents the frequency of $R_{0,i\text{-pseudo}}$ zero.

zeros are included in the calculation of variance, it results in an overestimation of variance. This shows that the jackknife technique will generate biologically unrealistic $R_{0,i\text{-pseudo}}$, which results in an overestimation of variances of the net reproductive rates. The overestimation of variances consequently makes 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 variance 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 variance. Because there are many problems associated with female life tables and analyses based on adult age (Chi and Liu 1985; Chi 1988; Yu et al. 2005; Chi and Su 2006; Huang and Chi 2012), 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 experiments in this study showed, however, that the variability in developmental rate, survival and reproduction of a life table could not be properly assessed with the jackknife method. For this reason and many others, the prediction of population dynamics under field conditions is difficult. In this study, we limit our discussion to the application of jackknife method to the net reproductive rate. There are other resampling methods, for example, 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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