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ORIGINAL ARTICLE

Age-stage, two-sex life tables of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) with a discussion on the problem of applying female age-specific life tables to insect populations

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Abstract Age-stage, two-sex life tables of the melon fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), reared on cucumber (*Cucumis sativus* L.), sponge gourd (*Luffa cylindrica* Roem) and a carrot medium (mashed *Daucus carota* L. mixed with sucrose and yeast hydrolysate) were constructed under laboratory conditions at 25 ± 1°C, 65% ± 0.5% relative humidity, and a photoperiod 12 : 12h (L : D). The intrinsic rates of increase of *B. cucurbitae* were 0.144 6, 0.141 2 and 0.068 8 days on cucumber, sponge gourd, and carrot medium, respectively. The highest net reproduction rate was 172 offspring per fly reared on sponge gourd. The mean generation times of *B. cucurbitae* ranged from 34 days reared on cucumber to 56 days reared on carrot medium. The life history raw data was analyzed using the traditional female age-specific life table and compared to results obtained using the age-stage, two-sex life table. When the age-specific female life table is applied to an age-stage-structured two-sex population, survival and fecundity curves will be improperly manipulated due to an inability to include variation in preadult development time. We discussed different interpretations of the relationship between the net reproductive rate and the intrinsic rate of increase to clarify possible misunderstanding in the literature.

Key words *Bactrocera cucurbitae*, *Cucumis sativus*, *Daucus carota*, life table, *Luffa cylindrica*

Introduction

The melon fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), is one of the most important pests in Taiwan, as well as in many regions in Asia (Koyama *et al.*, 2004; Dhillon *et al.*, 2005). It has been reported as a pest of 81 host plants (Dhillon *et al.*, 2005) and is listed as a quarantine pest in many countries (CABI & EPPO, 1997). In Taiwan, relevant agencies have set up integrated and cooperative control programs for the management of this pest during the last two decades, primarily using insecticide-baited cue-lure traps to control male melon flies. Although the government has invested enormous funds on control of the fly, it remains as a major pest in Taiwan. Meanwhile, with the increasing awareness of problems associated with pesticide use and the increased popularity of organic farming, development of consumer-protective and ecology-committed control strategies have become the main goal of pest management.

For an ecologically sound integrated pest management program, it is crucial to thoroughly understand the ecology of the pest. The life table generates an integrated

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and comprehensive description in details of development, survival, fecundity and life expectancy of a population, and is often used by scientists as a means of projecting the growth of populations (Chi, 1990). Because insects are ectothermic organisms, numerous difficulties can potentially occur when collecting data for the life tables of insect populations under different conditions. In order to understand the biological potential of pest populations, and to exclude variations of biotic and abiotic factors as much as possible, it is necessary to collect data for their life tables under controlled laboratory conditions and in the field. Information so obtained can be invaluable when attempting to elucidate the basic ecology of pest species.

In the development of life table theory, the traditional age-specific life table (Lotka, 1907; Lewis, 1942; Leslie, 1945; Birch, 1948) deals with only the female age-specific population, while ignoring males, the stage differentiation, and the variable developmental rate among individuals. For most insects though, developmental rates differ between the sexes and among individuals (Istock, 1981; Carey, 1993). Chi & Liu (1985) pointed out that neglecting the variable developmental rate and male population may cause errors in calculating demographic parameters, such as the intrinsic rate of increase, net reproductive rate and the mean generation time. Chi & Liu (1985) and Chi (1988) developed an age-stage, two-sex life table to take the stage differentiation and the male population into consideration. Based on the age-stage, two-sex life table, Chi & Getz (1988) constructed a mass-rearing program for stage-structured populations. Timing of control of pest populations is possible using the age-stage, two-sex life table (Chi, 1990). Furthermore, mathematical proofs demonstrating the correctness of applying the age-stage, two-sex life table to insect populations were provided by Yu *et al.* (2005) and Chi & Su (2006).

This paper provides essential basic information on the life stages and ecology of the melon fly by several means. First, because the supply of natural host, that is, cucumber (*Cucumis sativus* L.), is seasonally limited, to ensure a continuing year-round supply of viable laboratory-reared melon flies, it was necessary to study a readily available and durable natural material, that is, carrot, as a potential artificial medium for mass rearing of flies. We compared the demographic traits of flies reared on carrot with those reared on their natural hosts, cucumber and sponge gourd (*Luffa cylindrica* Roem). Life table study on sponge gourd is important, not only because it is a major crop in Taiwan, but also because sponge gourds are left in the field when the price is low and serve as an important reservoir for melon flies. Second, to graphically illustrate the differences between the age-stage, two-sex life table and the female age-specific life table, we analyzed our data using a traditional female life table. Because numerous errors in data analysis and interpretation of life table parameters exist in the literature, we explain the reasoning involved in life table analysis, and discuss some common misinterpretations in insect demographic studies. Finally, we used survival rate and fecundity data to project the melon fly population to show the advantage of using a two-sex life table in revealing the stage structure of insect populations.

Materials and methods

Life table study

Colonies of melon fly, *B. cucurbitae* (Coquillett) (Diptera: Tephritidae), were obtained from the Agricultural Research Institute Taichung, Taiwan, where flies have been continuously reared in the laboratory for over 100 generations with fecundity monitored. There is no significant difference in fecundity between laboratory-reared and wild flies (Y.B. Hwang, unpubl. data). Flies were kept on cucumber (*Cucumis sativus* L.), sponge gourd (*Luffa cylindrica* Roem), and a carrot medium (mashed carrot:sucrose:yeast hydrolysate = 2 : 1 : 1 in weight) in the laboratory at room temperature (ca. 25 ± 1°C) for two generations before the life table study. To facilitate egg collection, we cut cucumber, sponge gourd and carrot into thin slices (ca. 1mm), and then placed these in piles of 3–4 slices in the respective rearing cage to allow females to oviposit. After 24h, the piled slices were separated using forceps and 100 eggs were collected for the life table studies on sponge gourd and carrot medium; 62 eggs were collected for the cucumber study. Each egg was placed on fresh rearing medium (sliced cucumber or gourd or carrot medium) in individual Petri dishes and kept in growth chambers (25 ± 1°C, 65% ± 5% relative humidity [RH] and a photoperiod of 12:12h [L:D]). The survival of individual *B.cucurbitae* was recorded daily and fresh slices of cucumber, sponge gourd and carrot medium were supplied to avoid fungal growth. Mature larvae can be distinguished by their jumping behavior and were moved using a camelhair brush to plastic cups containing sawdust as pupation medium. After the emergence of adults, we paired one male with one female and kept them in inverted plastic cups (13 cm height, 9 cm diameter) placed on a Petri dish. Water was supplied by dipping a piece of cotton wool as a wick in a glass vial (1.5 cm diameter, 5.5 cm height) filled with water. Granulated sucrose (0.5 g) and yeast hydrolysate (0.5 g) were offered in a small plastic dish (3.5 cm diameter). We supplied fresh

slices of cucumber, sponge gourd or carrot for oviposition and recorded the fecundity daily until the death of all individuals. Voucher specimens of *B.cucurbitae* have been deposited in the Department of Entomology, National Chung Hsing University, Taichung, Taiwan.

Demographic analysis

Age-stage, two-sex life table Raw data of all individuals were analyzed according to the age-stage, two-sex life table theory (Chi & Liu, 1985; Chi, 1988). The age-stage specific survival rate (s_{xj}) (where x = age in days and j = stage; the first stage is the egg-larva stage, the second stage is the pupal stage, the third and fourth stages are the female and male, respectively), the age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), the age-specific fecundity (m_x), and the population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase, $\lambda = e^r$; R_0, the net reproductive rate; T, the mean generation time) are calculated accordingly. The intrinsic rate of increase is estimated by using iterative bisection method from:

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

with age indexed from 0 (Goodman, 1982). In the age-stage, two-sex life table, the l_x and m_x are calculated as:

$$l_x = \sum_{j=1}^{k} s_{xj} \qquad (2)$$

and

$$m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}}, \qquad (3).$$

where k is the number of stages (Chi & Liu, 1985).

Because life table study is extremely time-consuming and replication is impractical, we used the jackknife method (Sokal & Rohlf, 1995) to estimate the means and standard errors of the life table parameters. The mean generation time was defined as the length of time that a population needs to increase to R_0-fold of its size at the stable age-stage distribution and was calculated as $T = (\ln R_0)/r$. The age-stage life expectancy (e_{xj}) for individuals of age x and stage j was calculated according to the method described in Chi & Su (2006). To ease the raw data analysis, a computer program, TWOSEX-MSChart for the age-stage, two-sex life table analysis (Chi, 2008a), was designed in Visual BASIC (version 6, service pack 6) for Windows, and is available from the corresponding author and at http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey). We used the Tukey-Kramer procedure (Dunnett, 1980) to compare the difference among treatments following the description of Sokal & Rohlf (1995).

Female age-specific life table To demonstrate the differences between the female age-specific life table and the two-sex life table, we also analyzed our data using the traditional female age-specific life table. In the construction of a female age-specific life table, it is necessary to calculate the age-specific survival rate (l_x) and the age-specific fecundity (m_x) based on "female" individuals, where m_x is the mean number of female eggs laid per female adult at age x (counted from age 0). To calculate m_x, the total eggs laid by females at age x is used as dividend and the total number of female adults as divisor. If some females produce eggs at age x, while other individuals are still in preadult stages at the same age x, this causes a problem in the calculation of m_x. Moreover, because the sex of the individuals dying before the adult stage is unknown and the female age-specific life table cannot take the difference in developmental time among individuals into consideration, it is generally assumed that all female adults emerge at the same age. It is also the reason why the "adult age" is frequently used to construct l_x and m_x in many female life table studies (e.g., Lashkari *et al.*, 2007; Golizadeh *et al.*, 2008). Following these assumptions, the female age-specific fecundity (m_x) is 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. Furthermore, because the sexes of individuals that died during the preadult stages were unknown, we construct three survival curves to reveal the effect of inclusion or exclusion of preadult mortality on the life table: (i) the survival curve based on only individuals that emerged successfully as adult females, that is, we excluded the preadult mortality from the life table analysis; (ii) the survival curve including all females and half of individuals dying in the preadult stages, that is, we assumed a sex ratio of 1 : 1 for the preadult mortality; and (iii) the survival curve including all emerged females and all individuals dying in the preadult stages, that is, all preadult mortality is female.

Population projection

We used Timing-MSChart (Chi, 2008b) to project the population growth on three rearing media with an initial population of 100 eggs to reveal the growth and age-stage structure of *B. cucurbitae*.

Results

Age-stage, two-sex life table of B. cucurbitae

Because of the short egg duration and difficulty in determining the larval stages, we grouped the egg and all larval stages as the egg-larval stage. The pupation rates were 79%, 64%, and 70%, on cucumber, sponge gourd and carrot medium, respectively. The developmental times of egg-larval stage on both cucumber and sponge gourd were 7.4 days, which were significantly shorter than that reared on the carrot medium (8.5 days) (Table 1). The *B. cucurbitae* pupal stage reared on cucumber (7.7 days) was significantly shorter than that on sponge gourd and carrot medium (Table 1). The number of emerged males and females showed that the sex ratio was close to 1 : 1 in all three media. The adult preovipositional periods (APOP), that is, the duration from adult emergence to first oviposition, were significantly shorter in flies reared on cucumber and sponge gourd than those reared on carrot medium. There was no significant difference between the APOP of flies reared on cucumber and sponge gourd. However, the total preovipositional period (TPOP), that is, the duration from egg to first oviposition, of flies reared on cucumber is significantly shorter than those reared on sponge gourd and carrot medium. The age-stage specific survival rates (s_{xj}) (Fig. 1) shows the probability that a newborn will survive to age x and develop to stage j (Fig. 1). Due to the variable developmental rates among individuals, there are overlaps in the stage survival curves. By ignoring the stage differentiation, a single age-specific survival rate (l_x) gives the probability that an egg will survive to age x (Fig. 2). The age-stage specific fecundity (f_{x3}) gives the number of eggs produced by adult females (the 3rd stage) of age x, where the age x is counted from the egg stage. The curve of age-specific fecundity (m_x) (Fig. 2) shows that reproduction began at age 21 and 24 days on cucumber and sponge gourd, respectively. However, the first reproduction on

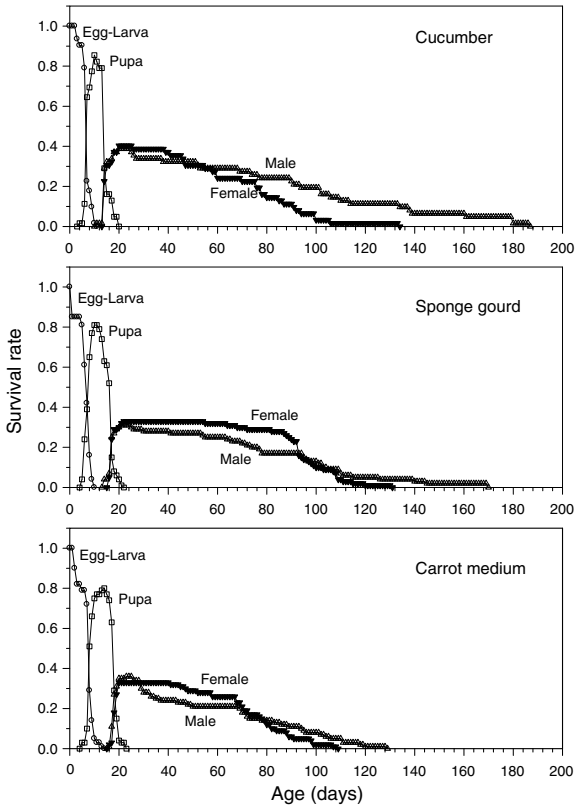

Fig. 1 Age-stage specific survival rate of *Bactrocera cucurbitae* fed on cucumber, sponge gourd and mashed carrot medium with sucrose and yeast hydrolysate at 25 ± 1°C, 65% ± 5% relative humidity, photoperiod 12 : 12h (L : D).

Table 1 Developmental time, longevity and fecundity of *Bactrocera cucurbitae* on *Cucumis sativus*, *Luffa cylindrica* and mashed carrot medium at 25 ± 1°C, 65% ± 5% relative humidity, photoperiod 12 : 12 h (L : D).

Stage	*C. sativus*		*L. cylindrical*		Carrot medium		df	*F*	*P*
	n	$\bar{x}$ ± SE	*n*	$\bar{x}$ ± SE	*n*	$\bar{x}$ ± SE			
Egg-larva (days)	53	7.4 ± 0.2 a	81	7.4 ± 0.1 a	80	8.5 ± 0.2 b	2,211	16.7	<0.0001
Pupa (days)	49	7.7 ± 0.1 a	64	9.9 ± 0.1 b	70	9.8 ± 0.1 b	2,180	116.0	<0.0001
APOP (days)	25	8.0 ± 0.4 a	33	9.6 ± 0.4 a	34	28.0 ± 1.8 b	2,82	104.1	<0.0001
TPOP (days)	25	23.1 ± 0.6 a	33	27.0 ± 0.5 b	34	46.6 ± 1.8 c	2,82	120.7	<0.0001
Adult (male) (days)	24	84.0 ± 10.0 a	31	73.5 ± 6.6 a	36	50.1 ± 5.6 b	2,88	6.1	0.00343
Adult (female) (days)	25	57.8 ± 5.1 a	33	77.7 ± 2.7 b	34	55.4 ± 3.4 a	2,89	12.1	<0.0001
Fecundity (eggs/♀)	25	341.8 ± 55.7 a	33	522.1 ± 24.9 b	34	137.5 ± 17.3 c	2,89	38.7	<0.0001

APOP, adult preovipositional period; TPOP, total preovipositional period (from egg to first oviposition). Means in the same row followed by the same letter are not significantly different ($P > 0.05$) using Tukey-Kramer procedure.

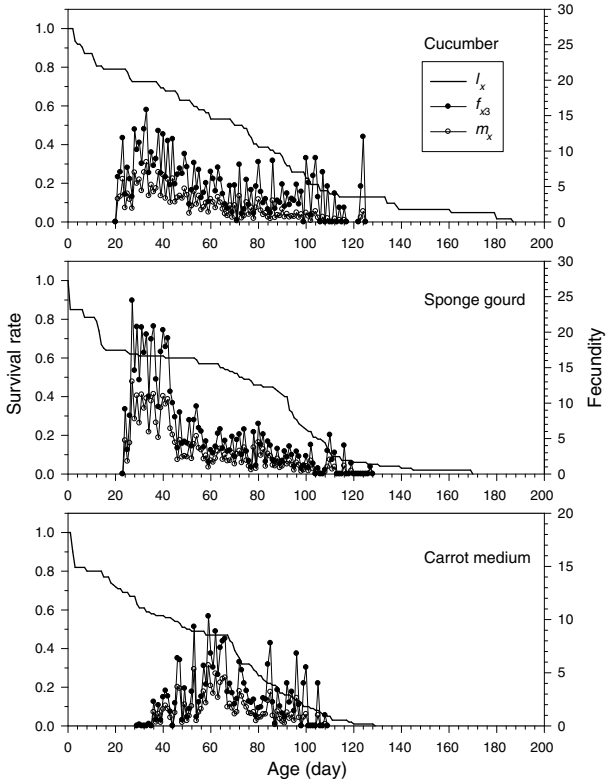

Fig. 2 Age-specific survival rate (l_x), age-stage specific fecundity (f_{x3}), age-specific fecundity (m_x) of *Bactrocera cucurbitae* fed on cucumber, sponge gourd and mashed carrot medium with sucrose and yeast hydrolysate at 25 ± 1°C, 65% ± 5% relative humidity, photoperiod 12 : 12 h (L : D).

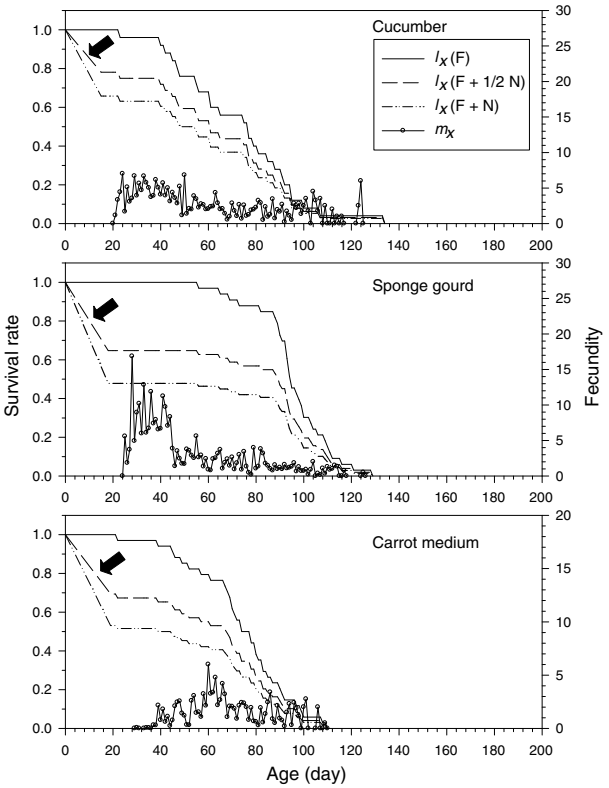

Fig. 3 Age-specific survival rate (l_x) and age-specific fecundity (m_x) of *Bactrocera cucurbitae* analyzed based on female age-specific life table (F, female adults; N, individuals died before adult stage.)

carrot medium was at age 30 days. The ovipositional period of *B.cucurbitae* lasted as long as 100 days on both cucumber and sponge gourd, but was as short as 80 days for flies reared on carrot medium. The maximal daily oviposition rates on cucumber and sponge gourd were much higher than that on carrot medium (Fig. 2).

Female age-specific life table of B. cucurbitae

To show the difference between the traditional female life table and the age-stage, two-sex life table, we also analyzed the raw data using the female life table. Because the female life table is incapable of considering the stage differentiation and the m_x is expressed as female offspring per female, we used the mean duration of preadult stage and assumed all females emerged at the same age (Fig. 3). Both l_x and m_x are different from those obtained by using the age-stage, two-sex life table. We have to point out that these curves are results of improper manipulation based on the assumption that all adults emerged at the same time. We will give detailed reasoning in the Discussion section.

Life expectancy, population parameters and reproductive value

Based on the age-stage, two-sex life table, the age-stage-specific life expectancy (e_{xj}) gives the expected life span an individual of age x and stage j can live after age x (Fig. 4). For example, the life expectancy of a newborn was 69 days on cucumber and a female of age 60 days will still be able to live for another month. The highest intrinsic rate of increase (0.144 6 days^{-1}) of *B. cucurbitae* was observed on cucumber and the lowest on the carrot medium (0.068 8 days^{-1}) (Table 2). The reproductive value (v_{xj}) is the contribution of individuals of age x and stage j to the future population (Fig. 5). The reproductive value for a new egg (v_{01}) is the finite rate of increase (λ), while peak reproductive value occurred at age 28 days on cucumber and 27 days on sponge gourd. This implies that, in comparison to other ages, female individuals of ages 28 and 27 dasys make the highest contribution to the population when reared on cucumber and sponge gourd, respectively.

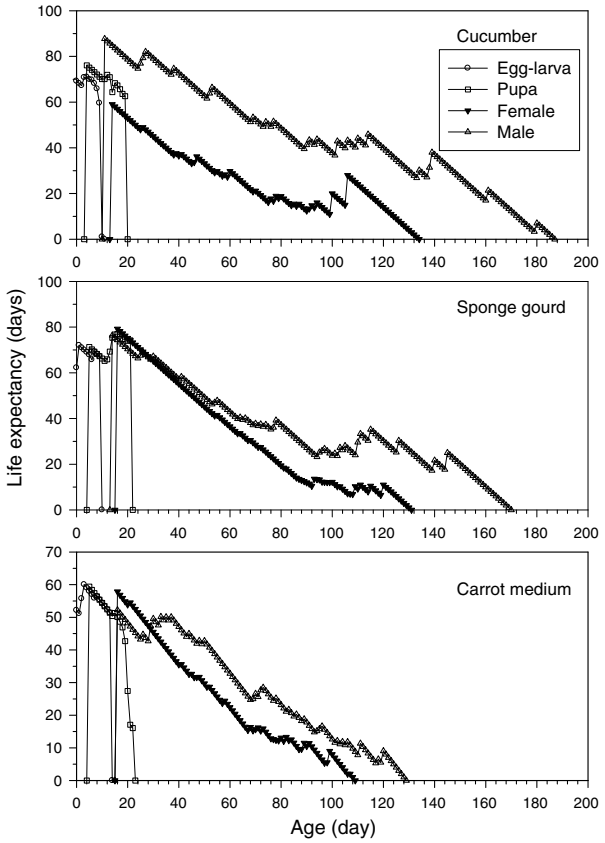

Fig. 4 Age-stage-specific life expectancy of *Bactrocera cucurbitae* fed on cucumber, sponge gourd and mashed carrot medium with sucrose and yeast hydrolysate at 25 ± 1°C, 65% ± 5% relative humidity, photoperiod 12 : 12h (L : D).

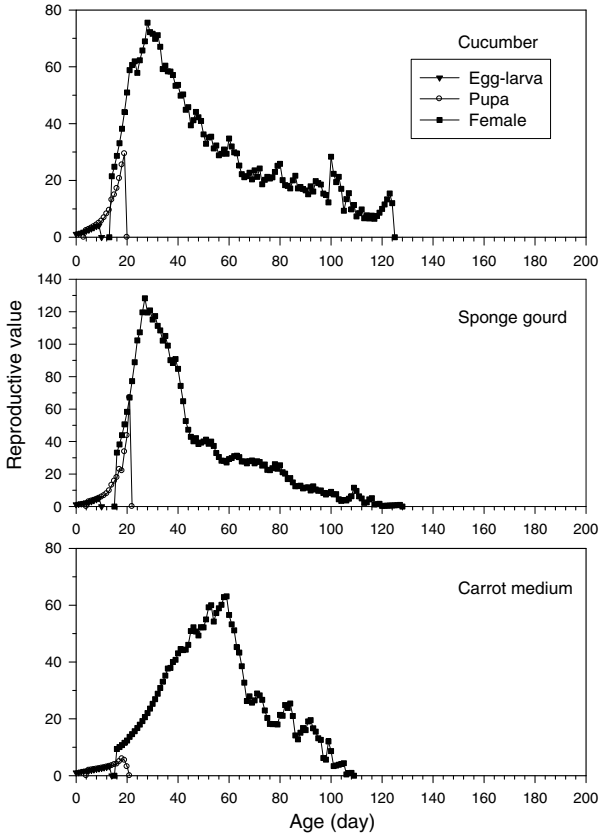

Fig. 5 Age-stage-specific reproductive value of *Bactrocera cucurbitae* fed on cucumber, sponge gourd and mashed carrot medium with sucrose and yeast hydrolysate at 25 ± 1°C, 65% ± 5% relative humidity, photoperiod 12 : 12h (L : D).

Discussion

Life table of Bactrocera cucurbitae

In our study, the egg-larval stage averaged 7.4 days on both cucumber and sponge gourd, and was within the range observed by Suenaga *et al.* (1992) in their study of larval jumping behavior. The total preadult development times of 15.1 days on cucumber and 17.3 days on sponge gourd were shorter than the 18–20 days reported by Miyatake (1993). Yang *et al.* (1994) reported the average duration of the egg, larval and pupal stages of *B. cucurbitae* on pumpkin, *Cucurbita moschata* (Duchesne) Duchesne ex Poiret, at 25°C as 1.3, 3.8 and 9.0 days,

Table 2 Population parameters of *Bactrocera cucurbitae* on *Cucumis sativus*, *Luffa cylindrica* and mashed carrot medium with sucrose and yeast hydrolysate at 25 ± 1°C, 65% ± 5% relative humidity, photoperiod 12 : 12h (L : D).

Population parameters	*C. sativus*	*L. cylindrica*	Carrot medium	df	*F*	*P*
Intrinsic of increase (r) (days^{-1})	0.1446 ± 0.0071 a	0.1412 ± 0.0053 a	0.0688 ± 0.0045 b	2, 259	65.6	<0.0001
Finite rate of increase (λ) (days^{-1})	1.1555 ± 0.0082 a	1.1517 ± 0.0061 a	1.0712 ± 0.0048 b	2, 259	65.6	<0.0001
Gross reproduction rate (*GRR*) (offspring)	227.0 ± 54.7 a	309.5 ± 39.6 a	114.9 ± 20.0 b	2, 259	8.0	0.00043
Net reproduction rate (R_0) (offspring)	137.8 ± 30.9 a	172.3 ± 26.0 a	46.8 ± 8.8 b	2, 259	9.7	<0.0001
Mean generation time (T) (days)	34.2 ± 0.9 a	36.5 ± 0.6 a	56.1 ± 1.7 b	2, 259	99.9	<0.0001

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

respectively. Vargas *et al.* (1996) noted that the development of the egg, larval and pupal stages of *B. cucurbitae* on wheat diets lasted 1.3, 6.6 and 10.2 days at 24°C, respectively. Vayssières *et al.* (2008) reported a total development time of *B.cucurbitae* on cucumber as 17.2 and 13.2 days at 25 and 30°C, respectively. Jiang *et al.* (2006) observed a longer larval stage (12.09 days) and a shorter pupal stage (7.5 days) on cucumber at 30°C. These studies show the total preadult duration of *B. cucurbitae* ranged from 14 to 20 days at 24 to 30°C. The rapid development of *B. cucurbitae* is a major factor affecting the classification of the species as a major economic pest.

The mean longevity of cucumber-reared adult male *B. cucurbitae* flies was 84.0 days. This was shorter than the 133.6 days in Vargas *et al.* (1997), the 115.68 days in Jiang *et al.* (2006) and the 178 days in Vayssières *et al.* (2008). The mean longevity for female adults was 57.8 days, and was also shorter than the female longevity of 79.1 days in Vargas *et al.* (1997), the 91.59 days in Jiang *et al.* (2006) and the 182 days in Vayssières *et al.* (2008). These data suggest possible differences occurring among geographical populations, rearing conditions, and so on.

In our study, the mean fecundities of *B. cucurbitae* females at 25°C were 341 and 522 eggs reared on cucumber and sponge gourd, respectively. These figures were significantly higher than that obtained for flies reared on carrot medium (137 eggs). Miyatake (1996) reported a higher total fecundity ranging 1 208.5–1 499.9 eggs at generation 5 for L-line *B. cucurbitae*; but the total fecundity decreased to 447.7–476.4 eggs at generation 20. In Miyatake (1996), the mean of peak fecundity ranged from 146.4 to 164.9 (Table 1, Miyatake [1996]); however, the maximum of fecundity curves (*y*-axis, eggs laid per week/surviving females) was less than 150. This discrepancy may be due to the data analysis. Vargas *et al.* (1997) reported a net fecundity of 578.6 eggs at 24°C, while Jiang *et al.* (2006) recorded the mean fecundity for melon fly on cucumber as 895.65 eggs and on sponge gourd as 806.35 eggs.

Dhillon *et al.* (2005) reviewed the biology of the melon fly. Differences in the development and longevity in published papers may be due to the intrinsic characteristics of respective populations, rearing media and methods, physical conditions, genetic factors, number of generations in culture and other variables. These variations in life history data of the melon fly from different locations strongly suggest that life tables should be collected for local application.

Population parameters

Yang *et al.* (1994) reported the intrinsic rate (r) and net reproductive rate (R_0) as 0.108 3 days^{-1} and 72.9 eggs, respectively for *B. cucurbitae* reared on *C. moschata* (Duchesne). Vargas *et al.* (1997) reported r and R_0 as 0.148 and 264.5 females/generation at 24°C for *B. cucurbitae* reared on a wheat diet. In Jiang *et al.* (2006), r and R_0 were 0.073 8 days^{-1} and 94.08 eggs for *B. cucurbitae* reared on cucumber. Vayssières *et al.* (2008) reported r and R_0 as 0.13 days^{-1} and 456 eggs for *B. cucurbitae* reared on cucumber. The above population parameters were calculated using age-specific female life tables. In contrast, we used the age-stage, two-sex life table in our study. The values of R_0 were 137.8, 172.3 and 46.8 offspring for flies reared on cucumber, sponge gourd and carrot medium, respectively. The values of r were 0.144 6, 0.141 2, and 0.068 8 days^{-1} on cucumber, sponge gourd, and carrot medium, respectively. As Chi (1988), Yu *et al.* (2005), and Chi & Su (2006) discussed and proved, the problems in applying female age-specific life table to two-sex insect populations, show it is inappropriate to compare population parameters obtained by using different analytical methods and life table theory. We will discuss theoretical aspects of this in the section "Problems with using a female age-specific life table".

Pest capacity can be analyzed from many viewpoints, including population increase rate (reproductive quantity and duration), survival capability, alternative host plants and many others. The reproductive value (Fig. 4) predicts the contribution of an individual of age x and stage j to the future population (Fisher, 1930; Pianka, 1994). The curves of reproductive value reveal that *B. cucurbitae* possess high reproductive potential in both quantity (v_{xj} as high as 65 to 128) and duration (as long as 3–4 months). The meaning of reproductive value deserves more attention in pest management applications.

Lewontin (1965) pointed out that the age of first reproduction plays an important role on the intrinsic rate. If fecundity remains the same, an earlier reproduction (i.e., shorter preoviposition period) will accompany a higher intrinsic rate. In most literature the time from adult emergence to initial oviposition is used to calculate the preoviposition period, that is, the APOP in this paper. When APOP is used, the preadult developmental time is ignored, therefore the effect of the first reproduction age on intrinsic rate is not properly analyzed. On the other hand, the total preovipositional period (TPOP) is calculated from eclosion from the egg and the effect of first reproduction age on the intrinsic rate will be revealed as pointed out by Lewontin (1965). In our study, the TPOP of *B. cucurbitae* reared on cucumber, sponge gourd and carrot medium was, in ascending order, 23.1, 27.0 and 46.6 days, respectively, while the intrinsic rates of increase were, in descending order, 0.144 6, 0.141 2 and 0.068 8 days^{-1}, respectively. From the viewpoint of demography, our results

show that calculating the TPOP yields more meaningful statistic data than APOP does and is more consistent with Lewontin's (1965) concept.

Problems with using a female age-specific life table

Because the female age-specific life table cannot take the variation in developmental rate into consideration, the mean duration is generally used to construct the survival curve (e.g., Vargas *et al.*, 1997, 2000). This results in smooth diagonal line segments from one preadult stage to the next preadult stage in the survival curve. In Fig. 3, the arrows show the drop of survival rate from egg to adult stage that resulted from this improper assumption. There are similar phenomena in figures in Vargas *et al.* (1997, 2000).

With a detailed examination we can illustrate the problems that resulted from using improper analytical methods and demonstrate the difference between the age-specific female life table and the age-stage, two-sex life table. We discuss a few points as follows.

1. **Stage overlapping.** The stage overlapping (Fig. 1) can only be observed by using the age-stage, two-sex life table. When mean developmental times of each stage are used to partition the life history into different stages in an age-specific female life table, individual developmental variations are ignored. Such manipulation ignores the fact of variable developmental time among individuals and the resulting stage overlapping (Chi, 1988).
2. **Relationship between R_0 and r.** According to life table theory, if, and only if, $R_0 > 1$, then r is positive. 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 $R_0 >=< 1$ means $\lambda >=< 1$ and *vice versa.* In the well-known textbook *Ecological Methods* by Southwood and Henderson (2000), it states "Clearly, values of R_0 in excess of 1 imply an increasing population and of less than 1 a decreasing population; when $R_0 = 1$, the population will be stationary" (p.419, last paragraph). Clearly, if $R_0 > 1$, then $r > 0$. In other words, if $R_0 > 1$, then $r > 0$ and $\lambda > 1$. If $R_0 = 1$, then $r = 0$ and $\lambda = 1$. If $R_0 < 1$, then $r < 0$ and $\lambda < 1$. However, in the report by Vargas *et al.* (1997), R_0 was 1.5 for *B. dorsalis* and r was -0.0003. Similar errors can often be observed when the age-specific female life table is applied to a two-sex population. Such discrepancy is mainly due to the application of the female life table theory to age-stage, two-sex structured insect populations.
3. **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

$$R_0 = s_a w F, \tag{4}$$

where s_a is the preadult survival rate of females and w is the female proportion of offspring. By using a female age-specific life table, Jiang *et al.* (2006) reported F, R_0, s_a and w of *B. cucurbitae* on cucumber as 895.65 eggs/female, 94.08 offspring, 0.545 1 day^{-1}, and 0.56, respectively. These results are not consistent with the relationship shown in equation 4. In Jiang *et al.* (2006), the fecundities of *B. cucurbitae* on different hosts ranged from 806.35 to 895.65 eggs/female. These values are higher than ours. The intrinsic rates in their report, on the contrary, are much lower, ranging from 0.059 8 to 0.077 9 days^{-1}. Although a high R_0 value is not necessarily always accompanied by a high r-value, in most instances when an inconsistent relationship is found between R_0 and F, it can be traced to errors in calculating the l_x and m_x. Vayssières *et al.* (2008) reported a very high net reproductive rate of 456 for *B. cucurbitae* at 25°C by using adult life history, while the intrinsic rate was only 0.13 days^{-1}. This again may be partly due to the improper 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. If their raw data were analyzed using the age-stage, two-sex life table, all discrepancies would be resolved. 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.
4. **Life table based on adult age.** Miyatake (1996) compared life history traits of artificially selected lines of melon fly based on "adult" age. According to the discussions in previous paragraphs, if one used the "adult age" to construct the life table, he would be unaware of the improper manipulation of the survival and fecundity curves. Consequently, the interpretation of demographic traits based on an "adult life table" will result in a variety of problems. Because the stage differentiation due to metamorphosis is a major and fascinating characteristic of insects, many entomologists have constructed life tables based on "adult" age (e.g., Smith, 1993; Liu & Stansly, 1998; Chabi-Olaye *et al.*, 2001; Ohta &

Ohtaishi, 2004; Golizadeh *et al.*, 2008). This problem of "adult life table" is, therefore, especially worthy of attention in the entomological literature.

Application of life table data

Two types of information can be obtained through life table study: the basic data and the derived parameters. Intrinsic rate of increase and the mean generation time, are the derived parameters. They are calculated for a population by assuming it settles down to a stable age-stage distribution as the time approaches infinity. Although "infinity" is never realized, the intrinsic rate is a good parameter to reveal and compare the potential of insect populations under different treatments. However, their practical applications in pest management are limited. The basic data, that is, survival rate, fecundity and the net reproductive rate (R_0), on the other hand, describe the life history characteristics. In the demography, the survival rate and fecundity can be used in population projection to predict the growth trend, as well as the stage structure of population in the short-term or long-term future. For a stable and complete life table, for example, a human life table based on birth and death data for an entire country, projections for limited time periods are quite reliable, because the human life tables are well documented. We use "complete" life table to mean that the human life table is constructed based on the whole population. Governments can plan many policies based on population projections. Insurance companies can use life tables to calculate life insurance premiums. In Fig. 6, we demonstrated the advantage of population projection based on the age-stage, two-sex life table in revealing the stage structure. However, precise projections in the field are very difficult since insect life tables will vary significantly with temperature and many other environmental factors. However, these difficulties do not mean that entomologists should ignore life table study. On the contrary, more studies and effort are needed to take advantage of using life tables in descriptions of age-specific or age-stage survival rates and fecundity for practical applications.

Our life table results of *B. cucurbitae* on cucumber and sponge gourd demonstrated that melon fly populations are able to grow considerably faster on both of these fruits than they do on carrot medium. Due to its low cost, durable storage and easy preparation, carrot medium can be considered as a mass-rearing medium. Data obtained from two-sex life table studies of individuals reared on carrot medium can be used to project and manage the population growth in mass-rearing and harvesting systems. Reza Rassoulian *et al*. (2004) also investigated artificial diets for rearing melon flies during their study on applying sterile

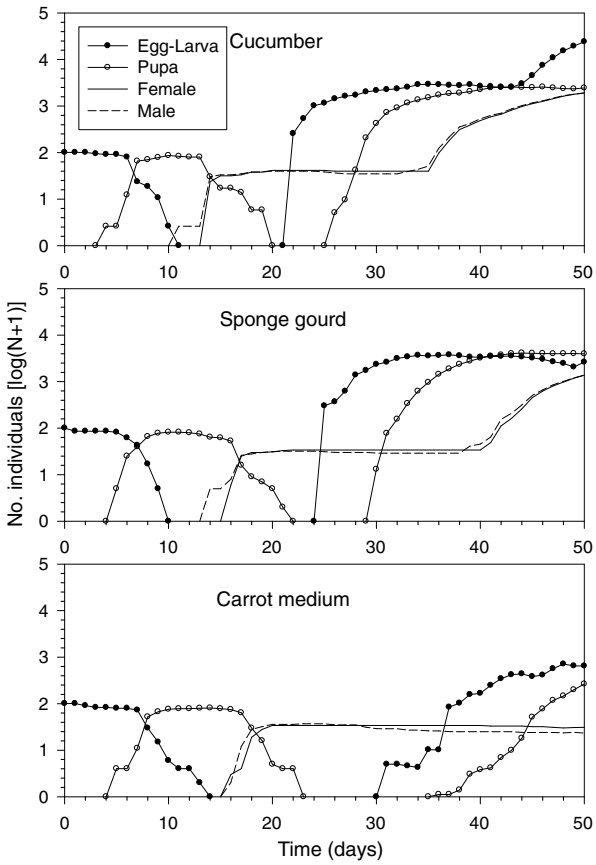

Fig. 6 Population projection showing the change of age-stage structure of *Bactrocera cucurbitae* during population growth.

male techniques for melon fly control. Because life tables give the most comprehensive information on a pest population, an ecologically sound management of the melon fly should integrate life table studies with other ecological studies. As the large difference between Figure 2 and 3 demonstrates, the application of the female age-specific life table to insect populations may cause problems. It is worthwhile to emphasize again that only correct data analysis will generate consistent and meaningful results, and subsequently, correct interpretation of the results. Moreover, the application of the age-stage, two-sex life table does include both sexes and takes the stage differentiation into consideration. In biological control studies, the effect of male predators can also be included. We recommend the age-stage, two-sex life table be used in insect demographic studies.

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