

## Demographic Analysis of Sex Ratio on Population Growth of *Bactrocera dorsalis* (Diptera: Tephritidae) With Discussion of Control Efficacy Using Male Annihilation

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### Abstract

The life table data for the oriental fruit fly, *Bactrocera dorsalis* (Hendel), at different adult sex ratios (1♀: 1♂, 1♀: 50♂, 50♀: 1♂ free-choice mating, and 50♀: 1♂ no-choice mating) were collected to determine the effects of sex-ratio manipulation on current pest control procedures. At 1♀: 1♂, females mated, on average, 2.3 times during their lifetime with a mean fecundity ( $F$ ) of 1,122 eggs. The net reproductive rate ( $R_0$ ), intrinsic rate of increase ( $r$ ), finite rate ( $\lambda$ ), and mean generation time ( $T$ ) were 561.0 offspring, 0.1693 d<sup>-1</sup>, 1.1844 d<sup>-1</sup>, and 37.4 d, respectively. At 50♀: 1♂ free-choice mating, males mated 46.7 times during their lifetime, while at 50♀: 1♂ no-choice mating, males mated on average 50 times during their lifetime, and all females mating only once in both treatments. The values for  $F$ ,  $r$ , and  $\lambda$  were significantly lower for both 50♀: 1♂ treatments than those in the 1♀: 1♂ group; the  $R_0$  values, however, were either equal to or even higher than those in the 1♀: 1♂ treatment. In the male-biased sex ratio (1♀: 50♂), fecundity was the highest (1,610 eggs) and female average life span the longest (166 d), while the  $R_0$  was the lowest (31.6 offspring) among all treatments. Population projections showed that even at a sex ratio of 50♀: 1♂, *B. dorsalis* could still produce a large number of offspring. These findings demonstrate that management strategies for controlling *B. dorsalis* could be properly evaluated by using demographic methods. Because female annihilation appears to be a more effective control strategy, it should be considered as a viable alternative.

**Key words:** *Bactrocera dorsalis*, sex ratio, life table, population projection

The oriental fruit fly, *Bactrocera dorsalis* (Hendel), has been recorded from >150 host plant species (White and Elson-Harris 1992) and is one of the most serious pests of fruit trees including guavas (*Psidium guajava* L.), carambola (*Averrhoa carambola* L.), wax apples (*Eugenia javanica* Lam.), mango (*Mangifera indica* L.), peaches (*Prunus persica* L.), pears (*Pyrus communis* L.), and citrus (*Citrus reticulata* Blanco). Their mating frequency and behavior, and the role of sex pheromones have been studied extensively (Miyatake and Haraguchi 1996, Alyokhin et al. 2001). A successful mating may last for 2 h or longer, and the sperms stored in the spermathecae will be viable and available for oviposition for the remainder of the female's life span (Arakaki et al. 1984, Alyokhin et al. 2001, Benelli et al. 2012). Multiple mating may occur, increasing the genetic variability and fecundity (Bateman 1972).

The successful application of male annihilation technique (MAT) and the sterile insect technique (SIT) have been implemented

against many fruit fly species. Since Steiner (1952) initially reported the successful control of the oriental fruit fly using methyl eugenol in the MAT, the MAT has been used worldwide in the management of fruit flies. The eradication of the oriental fruit fly in the semi-isolated 33-square-mile island of Rota, Mariana Islands, was achieved in 1965 (Steiner et al. 1965). The similar success was also reported in a papaya orchard in Hawaii, with an achievement of a 99%+ reduction in the male population; however, the fruit infestation rate was only reduced 48%, as the surrounding vegetation was not trapped (Cunningham and Suda 1986).

Since the successful screwworm eradication program (Baumhover et al. 1955, Knipling 1955, 1985; Vargas-Terán et al. 2005), the SIT has been widely used to control many fruit fly species (Pereira et al. 2013) including *Bactrocera dorsalis* (Hendel), *Bactrocera tryoni* (Froggatt) (Meats et al. 2002), *Ceratitidis capitata* (Wiedemann) (Shelly et al. 2007) as well a number of medically

important species, e.g., mosquitoes (Benedict and Robinson 2003) and tsetse flies (Vreysen et al. 2000, Vreysen 2001). Barclay et al. (2014) further demonstrated that simultaneous application of MAT and SIT techniques may potentially be an extremely powerful control strategy. In Taiwan, control of the oriental fruit fly using methyl eugenol could be dated to as early as 1940 (Lee 1988), while SIT was used between 1975 ~ 1984 and MAT has been used from 1984 until the present day. Although Chiu and Chu (1988) reported successful control of the oriental fruit fly using MAT on Lambay Island (located south-west to Taiwan), they subsequently reported that the fly had managed to reestablish itself on the Island shortly afterward (Chu and Chiu 1989).

Both MAT and SIT are the pest control strategies using sex-ratio manipulation (Robinson 1983). Factors affecting the success of sex-ratio manipulation, including the age of male flies (Wong et al. 1991), lek formation and male-male competition (Iwahashi and Majima 1986), sex ratio (Miyatake and Haraguchi 1996, Leftwich et al. 2012), host plants (Shelly and Villalobos 2004), and mating ratio (Horng and Plant 1993), were studied with different fruit fly species. These studies showed that each of these factors should be taken into consideration for a successful MAT and SIT program. Life tables are very useful and effective tools in evaluating the effects that sex ratio may have on growth and management of a given population, because they offer the most comprehensive and demographic analysis of the survival, development, and fecundity of the population. More importantly, however, they cover the entire life span of the population being studied. The life table parameters of *B. dorsalis* have previously been studied using traditional female, age-specific life tables (Yang et al. 1994; Vargas et al. 1996, 1997, 2000). Since female age-specific life tables completely ignore the male portion of the population, the effect of sex ratio on the population growth potential has been only partially evaluated. Chi and Liu (1985) and Chi (1988) developed the age-stage, two-sex life table theory to allow inclusion of both sexes, stage differentiation, and the variable developmental rates that typically occur among individuals. The age-stage, two-sex life table has been applied to many insect and mites populations (Atlihan and Chi 2008, Polat-Akköprü et al. 2015, Saadat et al. 2016, Tuan et al. 2016). Huang and Chi (2014) studied the life tables of *B. dorsalis* reared on different media using the age-stage, two-sex life table.

To assess the effect of sex-ratio manipulation on the population growth potential and its efficacy in pest management, we collected the life table data of *B. dorsalis* at different sex ratios. We then analyzed the effect of sex ratio on the survival of both sexes and the fecundity of females by using the age-stage, two-sex life table. Finally we used the life tables to project and compare the growth of populations developing from different sex ratios.

## Materials and Methods

### *Bactrocera dorsalis*

*Bactrocera dorsalis* individuals were originally collected from an abandoned orchard in Wufeng County, Taichung City, Taiwan, and have subsequently been reared in the laboratory on an artificial diet for >200 generations. The artificial diet, which was modified from that of Tanaka et al. (1969), consisted of: sodium benzoate (5 g), granulated sugar (240 g), yeast (140 g), HCL (20 ml), wheat shorts (480 g), and water (1,100 ml). Adults were reared in mass in 80 by 80 by 45-cm<sup>3</sup> cages and provided with an adult diet (sugar: yeast extract = 3:1). To collect eggs, we used plastic cups (5 cm in height, and 4.5 cm in diameter) in which 40 holes had been pierced

in the sides of the cup using a No. 1 insect pin. A cotton ball dipped in 10% guava juice was used to smear the inside of the cup. The cup was placed upside-down on a Petri dish (1.0 cm in height and 5.5 cm in diameter) inside the adult cage. Eggs were washed from the cup with distilled water and counted daily. Insects were kept in growth chambers set at 25 ± 1 °C, 70 ± 10% RH, and a photoperiod of 12:12 (L:D) h.

### Life Table Study

Pupae were collected from the mass-rearing colony. The emerging adults were allowed to oviposit and all eggs laid within a single 24-h period were collected. Flies were reared in groups before the pupal stage to conserve rearing space. After pupation, flies were kept separately in individual glass tubes (4.2 cm in length and 1.2 cm in diameter). The individually reared flies were then used in the following life table studies to determine the effects of different sex ratios. Emerging adults were transferred to an adult rearing cage (15 by 10 by 10 cm<sup>3</sup>). Every cage was supplied with fresh guava juice and adult diet for egg collection. Four treatments: 1♀: 1♂, 1♀: 50♂, 50♀: 1♂ (no-choice mating), and 50♀: 1♂ (free-choice mating) were used to study the effect of sex ratio on population parameters.

#### Sex Ratio 1♀: 1♂

Flies were paired and kept in individual adult cages (15 by 10 by 10 cm<sup>3</sup>). Fifty pairs were used for this ratio. The mating was checked daily and recorded for each pair during 18:00~22:00. The fecundity and survival were recorded daily until the death of all individuals.

#### Sex Ratio 1♀: 50♂

One female was kept with 50 males in an adult cage for 24 h. When a mating pair was detected, they were transferred to a new adult cage and kept together until death. The survival of the remaining 49 males was observed daily until the death of all individuals. Six replicates were carried out for this treatment.

#### Sex Ratio 50♀: 1♂ (no-choice mating)

A total of 300 female and six male adults were used in this treatment. To avoid overcrowding, 50 female adults were kept in an adult cage. Every day, a single female was randomly selected from the pool and allowed to mate with one male in a new cage. On the following day, the female was isolated in a rearing cage and its survival and fecundity were recorded daily until its death, while the male was allowed to mate with another female randomly selected from the female cage. This process was repeated until the death of all individuals.

#### Sex Ratio 50♀: 1♂ (free-choice mating)

A total of 300 female and six male adults were used in this study. Six sets of 50 females were kept in adult cages. Each day, a single male was released into each of the female cages. As soon as a mating pair was observed, they were removed and placed in a new adult cage. The following day, the female alone was transferred to a new cage and its survival and fecundity were recorded daily until death, while the male adult was returned to a female cage to mate with the remaining females. This process was repeated until the death of all individuals.

In this study, the eggs laid by each female at different ages were kept separately and the number of hatched eggs was recorded daily as the female age-specific fecundity (Mou et al. 2015).

## Life Table Analysis

The life history data were analyzed using the age-stage, two-sex life table theory (Chi and Liu 1985) and the method described by Chi (1988). We grouped the life history data into three stages: the egg-larval, pupal, and adult stages. The raw data were used to calculate the age-stage-specific survival rate ( $s_{xj}$ , where  $x$  = age in days and  $j$  = stage), age-stage-specific fecundity ( $f_{xj}$ ), age-specific survival rate ( $l_x$ ), age-specific fecundity ( $m_x$ ), age-stage life expectancy ( $e_{xj}$ ), age-stage reproductive value ( $v_{xj}$ ), adult preoviposition period (APOP), and total preoviposition period (TPOP). The estimated population parameters were the net reproductive rate ( $R_0$ ), intrinsic rate of increase ( $r$ ), finite rate of increase ( $\lambda$ ), and mean generation time ( $T$ ). In the age-stage, two-sex life table, the  $l_x$ ,  $m_x$ , and  $R_0$  values are calculated as:

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

$$m_x = \frac{\sum_{j=1}^k s_{xj} f_{xj}}{\sum_{j=1}^k s_{xj}} \quad (2)$$

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (3)$$

where  $k$  is the number of stages. The intrinsic rate of increase ( $r$ ) was estimated using the iterative bisection method from the Euler-Lotka formula with age indexed from 0 (Goodman 1982):

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (4)$$

The finite rate of increase ( $\lambda$ ) is calculated as  $\lambda = e^r$ . The mean generation time ( $T$ ) is defined as the length of time that a population needs to increase to  $R_0$ -fold of its population size at the stable age-stage distribution and is calculated as  $T = (\ln R_0)/r$ . The life expectancy ( $e_{xj}$ ) is the length of time that an individual at age  $x$  and stage  $j$  is expected to live and is calculated using the Chi and Su (2006) equation:

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{\beta} s'_{iy} \quad (5)$$

where  $s'_{iy}$  is the probability that individuals at age  $x$  and stage  $j$  will survive to age  $i$  and stage  $y$  and is calculated by assuming  $s'_{xj} = 1$ . Fisher (1930) defined the reproductive value as the contribution of an individual to the future population. In the age-stage, two-sex life table, the reproductive value ( $v_{xj}$ ) is calculated according to Tuan et al. (2014a, b) as:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{\beta} s'_{iy} f_{iy} \quad (6)$$

The computer program (TWOSEX-MSChart) was used in this analysis (Chi 2016b). The program, written in Visual BASIC for Windows OS is available at <http://140.120.197.173/Ecology/Download/TwoSEX-MSChart.rar>. The bootstrap technique (Efron and Tibshirani 1993; Huang and Chi 2012b) with 200,000 resampling was used to estimate the variances and standard errors of the population parameters. Different treatments were compared with the paired bootstrap method, which is embedded in the above computer program (TWOSEX-MSChart).

## Population Projection

The survival, development rate, and fecundity data collected in the life table study were used to simulate the growth and stage differentiation of the *B. dorsalis* population by using the computer program TIMING-MSChart (Chi 1990, 2016a). The population growth of the four sex ratio treatments was simulated using an initial population of 10 eggs.

## Results

At the sex ratio of 1♀: 1♂, the APOP and TPOP of females were 11.0 and 28.9 d, respectively (Table 1), with females mating an average of 2.3 times during their lifetime (Fig. 1). Significantly shorter APOP (7.7 d) and TPOP (25.8 d) values were observed in the 1♀: 50♂ treatments. In the 50♀: 1♂ treatments with free-choice and no-choice mating, both the APOP and TPOP were considerably longer than those in the 1♀: 1♂ and 1♀: 50♂ treatments (Table 1); all males mated with a virgin female almost every day and, on average, mated 46.7 times (free-choice mating) and 50 times (no-choice mating) during their lifetime (Fig. 1). The average male longevities of 84.3 d for no-choice mating and 88.7 d for free-choice mating were shorter than those in the 1♀: 1♂ sex ratio treatment. All females in the 1♀: 50♂ treatment produced offspring, while in the 1♀: 1♂ and 50♀: 1♂ (no-choice mating) treatments, 96~98% females produced offspring. In the 50♀: 1♂ (free-choice mating) treatment, however, ~10% of the mated females did not produce offspring. In the male-biased (1♀: 50♂) treatment, females laid eggs for an extended period of time (102.17 d), which was significantly longer than in other treatments (Table 1).

The age-specific survival rate ( $l_x$ ), age-stage-specific fecundity ( $f_{xj}$ ), age-specific fecundity ( $m_x$ ), and age-specific maternity ( $l_x m_x$ ) are presented in Fig. 2. In the 1♀: 1♂ and 1♀: 50♂ treatments, the  $f_{x3}$  values were higher than those in the female-biased treatments (50♀: 1♂). Reflecting the lower proportion of females, the  $m_x$  values in 1♀: 50♂ were the lowest among all treatments. Higher age-stage-specific fecundities (mostly >20 eggs) occurred during the age interval 25–50 d in both the 1♀: 1♂ and 1♀: 50♂ treatments. However, the age-stage-specific fecundities were lower (<15 eggs) in both the free-choice and no-choice mating options when the sex ratio was 50♀: 1♂.

The age-stage-specific life expectancies ( $e_{xj}$ ) of *B. dorsalis* in different treatments are plotted in Fig. 3. The life expectancy of a newborn egg (i.e.,  $e_{01}$ ) is equivalent to the mean longevity of all individuals. The values of  $e_{01}$  were 96.7, 74.9, 116.8, and 128.6 d for the 1♀: 1♂, 1♀: 50♂, 50♀: 1♂ (free mating), and 50♀: 1♂ (no-choice mating) treatments, respectively. In most treatments, life expectancy decreased with aging. However, in the treatment 1♀: 50♂, the life expectancy of a newly emerged female adult (i.e., age 17 d) increased to 148.7 d.

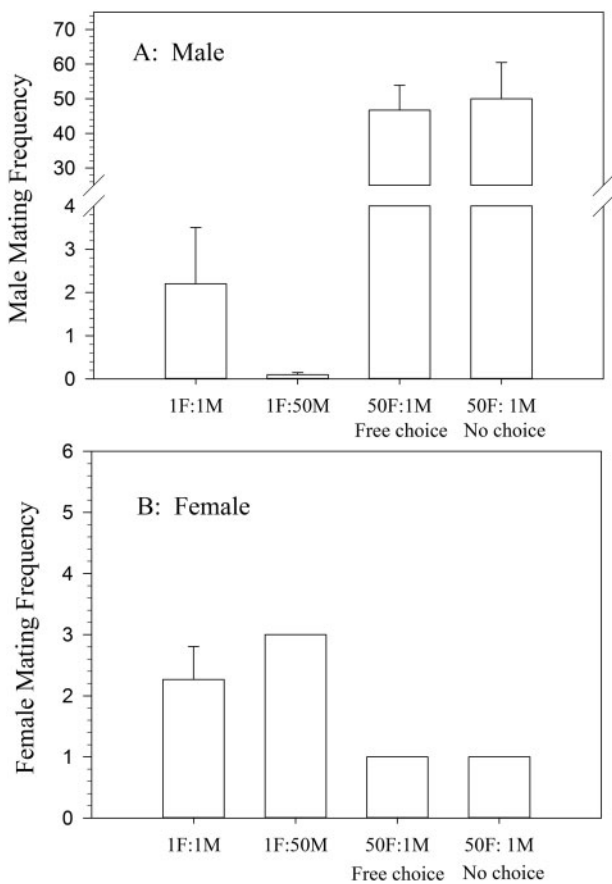
The reproductive values ( $v_{xj}$ ) of fruit flies at age  $x$  and stage  $j$  are shown in Fig. 4. The reproductive values significantly increased after the emergence of adult females. For example, at the sex ratio of 1♀: 1♂, the reproductive value for a new egg ( $v_{01}$ ) was the finite rate of increase ( $\lambda = 1.1844 \text{ d}^{-1}$ ). When a female adult emerged at age 16 d, the  $v_{xj}$  increased significantly to 35.6, and increased further to a value of almost 200 at age 29 d. The highest  $v_{xj}$  value (344) was observed for a female adult at age 26 d in the 1♀: 50♂ treatment. The reproductive values in the two female-biased treatments (50♀: 1♂ free mating and no-choice mating) were significantly lower than those in the 1♀: 50♂ and 1♀: 1♂ treatments.

The population parameters of *B. dorsalis* are listed in Table 2. The highest net reproductive rate ( $R_0$ ) was 687.9 offspring observed in the treatment 50♀: 1♂ with free-choice mating, while the lowest

**Table 1.** Means ( $\pm$ SE) of the adult preoviposition period (APOP, the time interval from female adult emergence to its first oviposition day), total preoviposition period (TPOP, the time interval from the birth of a female individual to the first oviposition day), fecundity, and longevity of the oriental fruit fly at different sex ratios

Treatments	n	Immature (d)	APOP (d)	TPOP (d)	Reproductive females (%)	Oviposition days (d)	Fecundity (eggs/female)	Total longevity (d)	
								Female	Male
1♀: 1♂	50	17.99 $\pm$ 0.08	11.0 $\pm$ 0.8c	28.9 $\pm$ 0.7c	97.83 $\pm$ 2.16ab	45.84 $\pm$ 5.10bc	1122 $\pm$ 123b	93.0 $\pm$ 5.6d	96.4 $\pm$ 5.6a
1♀: 50♂	6	18.19 $\pm$ 0.04	7.7 $\pm$ 0.2d	25.8 $\pm$ 0.5d	100 $\pm$ 0.00a	102.17 $\pm$ 11.1a	1610 $\pm$ 242a	165.7 $\pm$ 9.3a	73.1 $\pm$ 1.9c
50♀: 1♂ (Free-choice mating)	50	19.09 $\pm$ 0.02	33.2 $\pm$ 1.1b	52.3 $\pm$ 1.1b	89.33 $\pm$ 1.79c	41.83 $\pm$ 2.14b	702 $\pm$ 41c	117.3 $\pm$ 2.8c	88.7 $\pm$ 7.9ab
50♀: 1♂ (No-choice mating)	50	18.99 $\pm$ 0.00	44.4 $\pm$ 1.6a	63 $\pm$ 1.5a	96.00 $\pm$ 1.13b	36.45 $\pm$ 1.46c	578 $\pm$ 25d	129.5 $\pm$ 2.7b	84.3 $\pm$ 12.2bc

Means followed by the same letter in a column are not significantly different according to the paired bootstrap test at a 5% significance level. The standard errors were estimated using the bootstrap technique with 200,000 resampling.



**Fig. 1.** Mating frequencies (mean  $\pm$  SE) of *B. dorsalis* male (A) and female (B) adults in different sex ratio treatments (1F:1M, 1F:50M, 50F:1M-free choice mating, and 50F:1M-no choice mating; F: female, M: male).

value was 31.6 in the 1♀: 50♂ treatment. The highest intrinsic increase rate ( $r=0.1693\text{ d}^{-1}$ ) and finite rate ( $\lambda=1.1844\text{ d}^{-1}$ ) were obtained in the treatment 1♀: 1♂, with a generation time ( $T$ ) of 37.4 d. In the sex ratio treatment of 1♀: 50♂, the values of  $F$ ,  $R_0$ ,  $r$ ,  $\lambda$ , and  $T$  were 1,610 eggs, 31.6 offspring,  $0.0727\text{ d}^{-1}$ ,  $1.0754\text{ d}^{-1}$ , and 47.5 d, respectively. In the sex ratio treatment of 50♀: 1♂ with no-choice mating, the  $R_0$  was 566.6 offspring, which was not significantly different from that of the 1♀: 1♂ treatment; although the intrinsic rate ( $r$ ) ( $0.1199\text{ d}^{-1}$ ) was significantly lower. The mean

generation time ( $T$ ) in the 50♀: 1♂ treatment with no-choice mating was 52.9 d, which was significantly longer than the 37.4 d of the 1♀: 1♂ treatment. The net reproductive rate,  $R_0$  of 687.9 offspring in the 50♀: 1♂ treatment, was higher and significantly different from every other treatment. However, the intrinsic rate in the free-choice mating ( $r=0.1326\text{ d}^{-1}$ ) treatment was still significantly lower than in the 1♀: 1♂ treatment ( $r=0.1693\text{ d}^{-1}$ ). In general, the 50♀: 1♂ sex ratio resulted in a lower intrinsic increase rate, because only a single male was available, females were forced to wait to mate with the male and consequently produced eggs much later. The relationship between the mean fecundity ( $F$ ) and net reproductive rate ( $R_0$ ) was consistent with the proof given by Chi (1988), i.e.,  $R_0=(N_f/N)\times F$  in each of the treatments, where  $N_f$  is the number of female adults and  $N$  is the number of eggs used at the beginning of life table study.

**Population Projection**

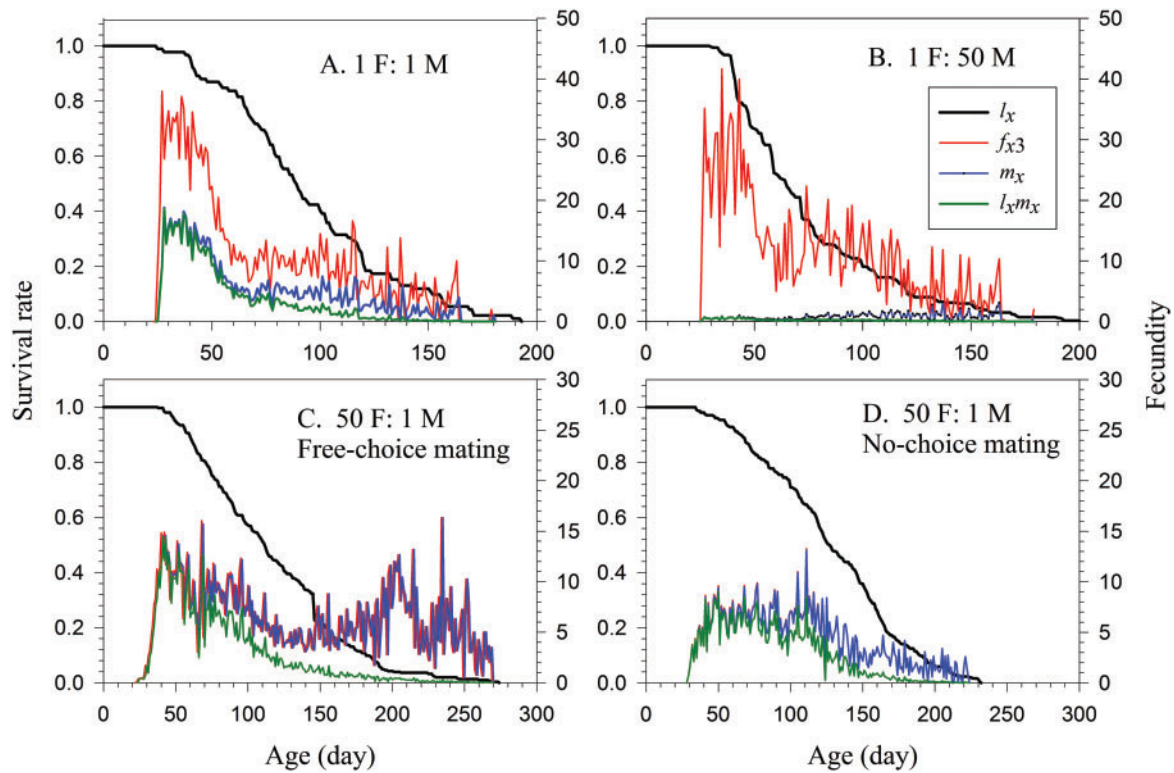
Although the simulated population projection showed that the sex ratio 1♀: 1♂ had the highest population growth potential (Fig. 5A), fruit flies in both of the female-biased sex ratios (50♀: 1♂, free-choice and no-choice mating) were still able to produce a high population of flies (Fig. 5C and D).

**Discussion**

**Effect of Sex Ratio on the Life Table of *B. dorsalis***

Gabre et al. (2005) showed that the TPOP determined from birth is a better parameter than the commonly used APOP because it included the effect the preadult developmental time has on the population growth rate. Therefore, TPOP should be the preferred statistical measure and is consistent with Lewontin’s (1965) concept that the age of the first reproduction plays an important role in the intrinsic rate. Vargas et al. (1997) reported that the adult preoviposition period of the oriental fruit fly was 7.3 d, which was shorter than the 11 d found in this study. However, based on the findings of Lewontin (1965) and Gabre et al. (2005), this difference cannot be properly compared without inclusion of the preadult developmental time. In both female-biased treatments (50♀: 1♂ free-choice mating and no-choice mating), the TPOP was significantly extended due to the limited number of males causing delays in the females’ ability to mate. In the 50♀: 1♂ no-choice mating treatment, the TPOP was twice as long as it was in the 1♀: 1♂ and 1♀: 50♂ treatments. The longer TPOPs consequently resulted in a significantly lower





**Fig. 2.** (A–D) Age-specific survival rate ( $l_x$ ), female age-specific fecundity ( $f_{x3}$ ), age-specific fecundity ( $m_x$ ), and age-specific maternity ( $l_x m_x$ ) of *B. dorsalis* in different sex ratio treatments (1F:1M, 1F:50M, 50F:1M-free choice mating, and 50F:1M-no choice mating; F: female, M: male).

intrinsic rate and finite rate of increase in the female-biased treatments.

It is interesting to note that the TPOP in the 50♀: 1♂ treatment with free-choice mating was significantly shorter than that in the 50♀: 1♂ no-choice mating treatment. As Wong et al. (1989) showed significant variation in age of sexual maturation occurring in both laboratory and wild populations, the female in the free-choice mating treatment can mate with a sexually matured male at a younger age or vice versa. Similarly, the TPOP in the 1♀: 50♂ treatment was significantly shorter than that in the 1♀: 1♂ group. These differences in TPOP demonstrate that female *B. dorsalis* flies are apparently able to distinguish appropriate mating partners when given sufficient choices (Iwahashi and Majima 1986, Wong et al. 1989).

The sex ratio also played an important role in longevity of both males and females. Papadopoulos et al. (2010) concluded that courting was responsible for the longevity reduction in *C. capitata*. Aigaki and Ohba (1984) reported a negative correlation between the mean life span of both sexes and the male density per vial for *Drosophila virilis* Sturdevant. Carey et al. (2002) showed that the virgin *C. capitata* flies experienced lower mortality than mated flies from eclosion to day 20, but higher mortality thereafter. Fanson et al. (2012) studied the cost of reproduction in the Queensland fruit fly (*Bactrocera tryoni* (Froggatt)) and concluded that the trade-off between life span and reproduction is mediated by the detrimental side effects of protein ingestion on their life span. All these studies showed that the life span of fruit flies could be affected by density, mating status, nutrients, etc. In the 1♀: 50♂ treatment of our study, males had a significantly shorter life span (73.1 d) than males in other treatments. Because the overwhelming majority of males in this treatment were unsuccessful in their frequent courting behavior with the single female provided during the first day, this may have partly contributed to the shorter life span observed in these males,

while the incapability of mating may also contribute to the shorter longevity in most males (Carey et al. 2002). On the other hand, the females from this group survived longer than in those in all other treatments. Lance and McInnis (2005) listed “female choice of mates” as one of the characteristics of insect mating systems that is important to SIT. The longer longevity of females in the 1♀: 50♂ treatment may have been due to the female choosing an optimal mate, and afterwards, the isolated pair was not exposed to the crowding effect and courting interference of other males. In the female-biased treatments (50♀: 1♂), females also survived longer than females in the 1♀: 1♂ treatment. The longer longevity in this case may stem from the fact that most females mated later and with older males, and were, therefore, required to dedicate less energy to reproduction. The extended longevity of the females is also evident in the life expectancy data (Fig. 3).

Using the age-stage, two-sex life table, allowed us to account for differences that occurred between individuals and between sexes to reveal their effects on population growth and potential pest management. These critical features would not have been observed if the traditional female-only life table had been applied. As Huang and Chi (2012a) demonstrated, application of the traditional female age-specific life table should be utilized only with special caution.

### Population Projection

Barclay and Hendrichs (2014) showed that the process of attracting and killing large numbers of males is a rather ineffective method for suppressing pest populations, although their model did show that the combination of attracting both males and females can be more effective. At the 1♀: 1♂ sex ratio both females and males can locate a mate efficiently without delay and rapid population growth would ensue. Because a single male *B. dorsalis* is able to mate with a

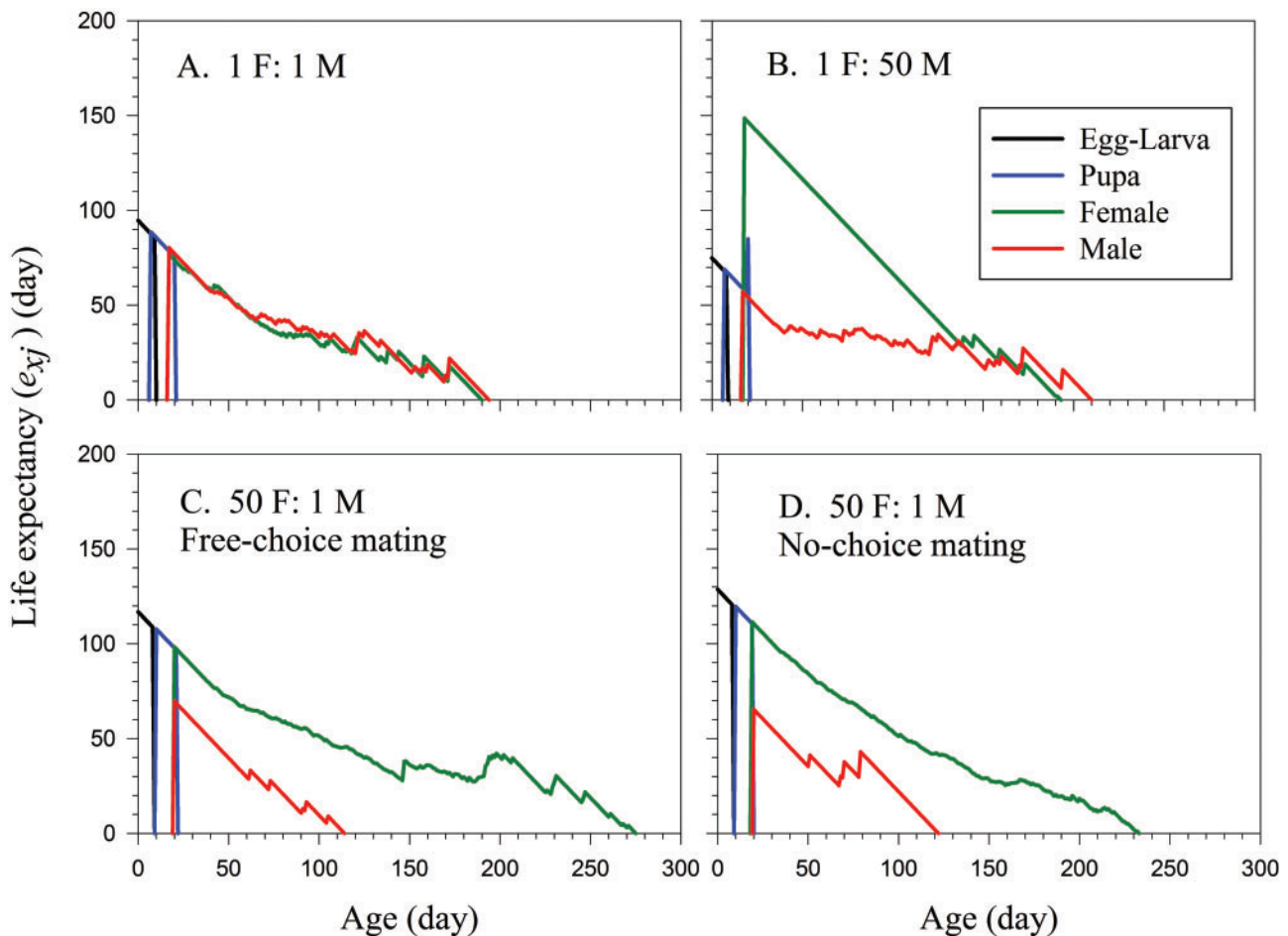


Fig. 3. (A–D) Age-stage-specific life expectancy ( $e_{xj}$ ) of *B. dorsalis* in different sex ratio treatments (1F:1M, 1F:50M, 50F:1M-free choice mating, and 50F:1M-no choice mating; F: female, M: male).

multitude of females even in a highly female-biased population (50♀: 1♂), the *B. dorsalis* population also showed a high growth potential (Fig. 5C and D) at this sex ratio. This demonstrates the limited efficacy of the male annihilation strategy. In contrast, in the male-biased treatment (1♀: 50♂), the population increase was the slowest among all treatments (Fig. 5B), showing that female annihilation would be a most efficient control technique.

Our results have shown that sex ratio is an important factor in pest management programs based on MAT, SIT, and other sex-ratio manipulation techniques. Because the effects of sex-ratio manipulation are complicated, the life table is a valuable tool for comprehensively evaluating populations. Our results demonstrated the following points: 1) Although both male- and female-biased sex ratios can reduce the population growth potential (the intrinsic rate and finite rate) of the fruit flies, the *B. dorsalis* population would still increase, because a single male is capable of mating with many females. An area-wide strategy, including the proper timing of the control plan, a continual attract-and-kill male program, an extended buffer zone, and provision of food bait, should be integrated into the management program (Hendrichs et al. 2007, Vargas et al. 2008). Additionally, the simultaneous application of MAT and SIT may be a more effective strategy as shown by Barclay et al. (2014), and should be seriously considered, if practical. 2) In the field, many newly emerged male adults are attracted to methyl eugenol after harvesting in an infested orchard, while gravid females disperse to other habitats due to lack of suitable substrate for oviposition

(Bateman 1972, Jang and Light 1991, Alyokhin et al. 2000, Cornelius et al. 2000, Muhammad 2015). Therefore, monitoring of *B. dorsalis* populations using methyl eugenol traps must be carefully considered, because the actual female density may not be accurately reflected by simply counting the number of trapped males. 3) Because previous female age-specific life tables ignored the male population, their usage in the male annihilation program should be critically reevaluated and reinterpreted. 4) Although the population projection showed that the male annihilation technique would initially reduce the female population, once the effect of the male annihilation is reduced, the pest population will quickly rebound. 5) Female annihilation may be a more efficient control strategy, and searching for effective female attractants or female-specific lethal genes (Chang et al. 2016) should be made a high priority. Each of the above findings is important in developing an effective, sustainable, and economic management program for *B. dorsalis*.

Many fruit fly species are currently known to cause serious agricultural losses in different crops and different regions of the world. Although they are taxonomically distinct, they share many features in common. Many of these shared factors need to be taken into consideration. Life tables are important tools for population ecology and pest management, because they offer the most comprehensive data covering the development, survival rate, stage and sex differentiation, and reproduction. Life table data can be used to project the population growth and adjust timing for effective pest control. However, as in many other experiments, life table data obtained

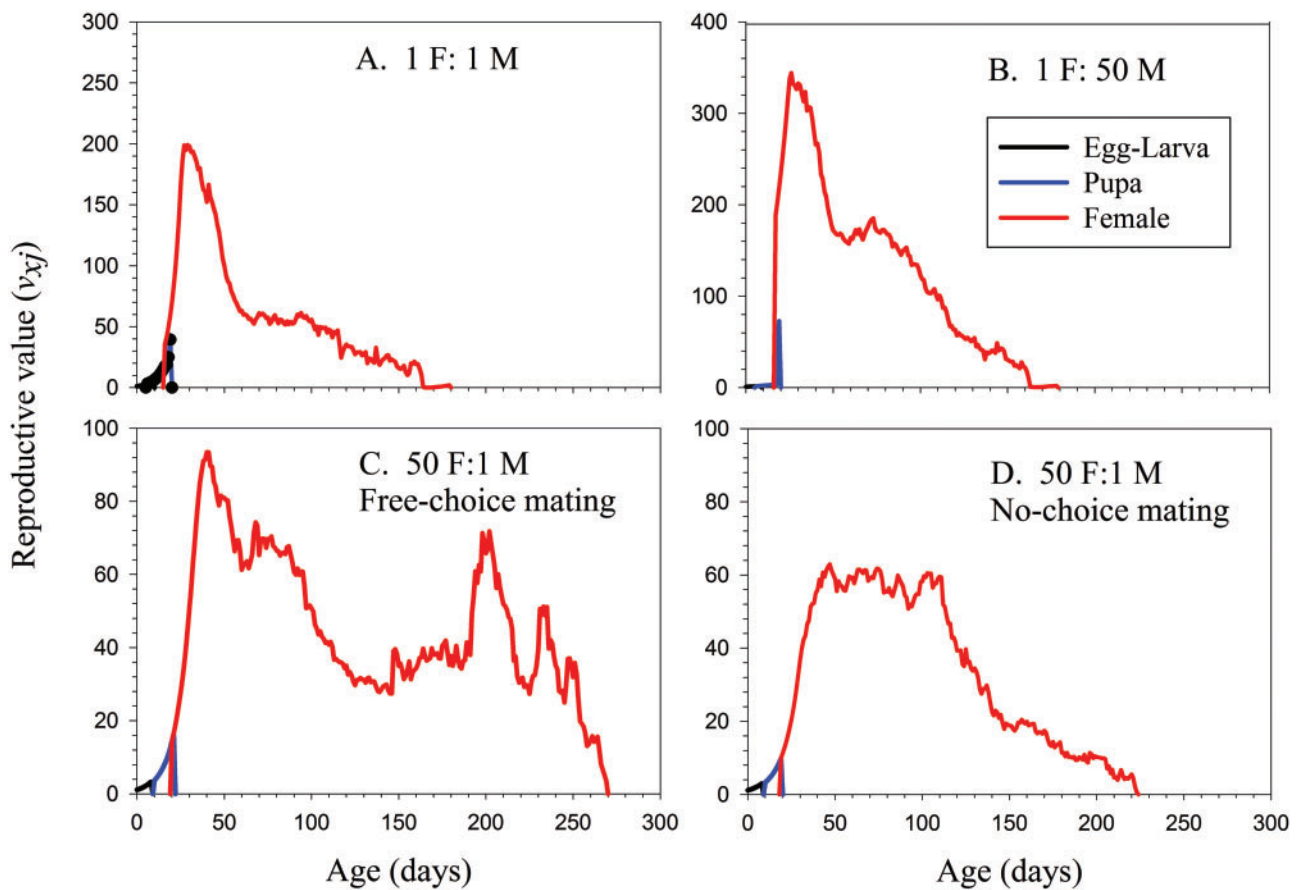


Fig. 4. (A–D) Age-stage-specific reproductive value ( $v_{xj}$ ) of *B. dorsalis* in different sex ratio treatments (1F:1M, 1F:50M, 50F:1M-free choice mating, and 50F:1M-no choice mating; F: female, M: male).

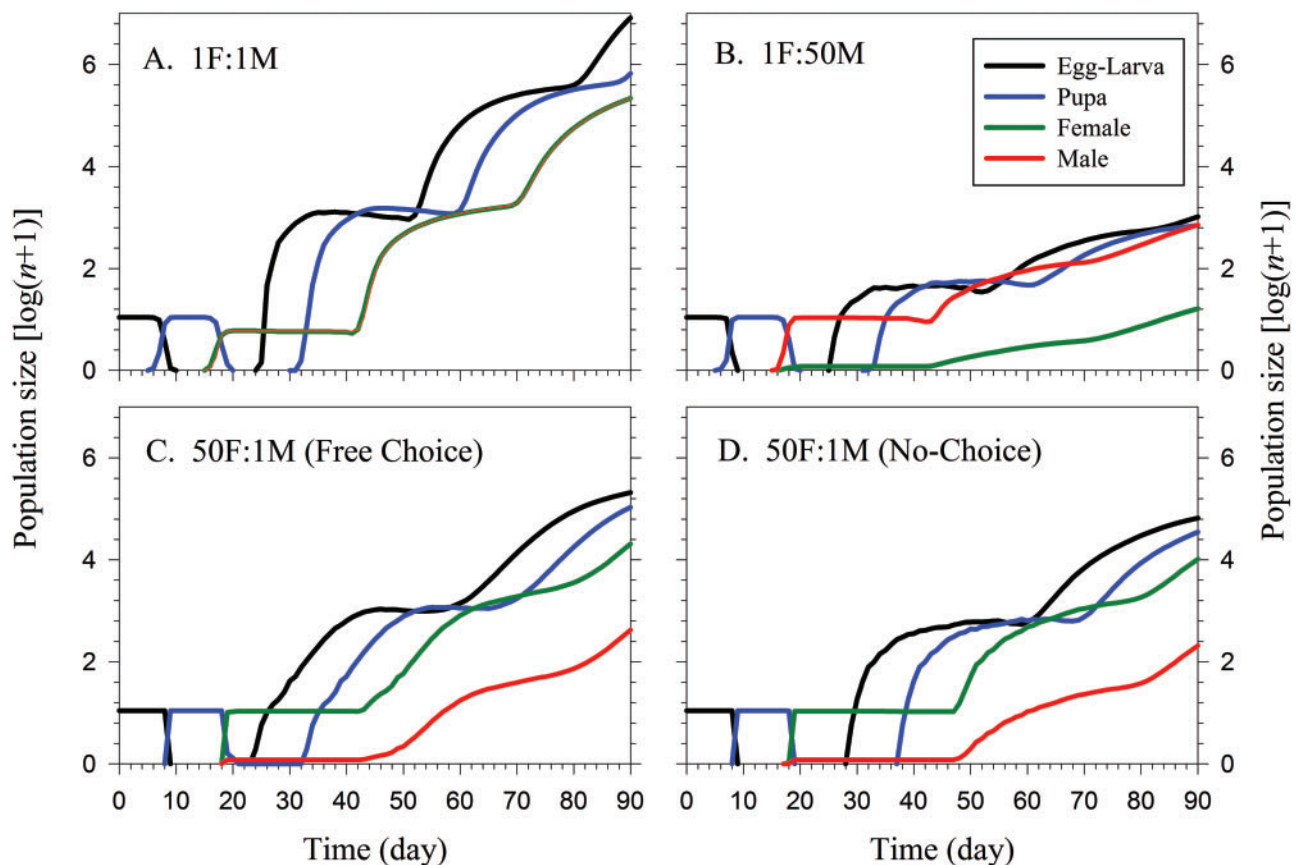
Table 2. Population parameters (means  $\pm$  SE) ( $R_0$ , net reproductive rate;  $T$ , mean generation time;  $r$ , intrinsic rate of increase;  $\lambda$ , finite rate) of *B. dorsalis* for different sex ratio treatments

Treatments	$n$	$R_0$ (offspring)	$T$ (d)	$r$ ( $d^{-1}$ )	$\lambda$ ( $d^{-1}$ )
1♀: 1♂	92	561.0 $\pm$ 84.9b	37.4 $\pm$ 0.6c	0.1693 $\pm$ 0.0047a	1.1844 $\pm$ 0.0055a
1♀: 50♂	306	31.6 $\pm$ 13.4c	47.5 $\pm$ 3.4b	0.0727 $\pm$ 0.0129d	1.0754 $\pm$ 0.0506d
50♀: 1♂ (Free-choice mating)	306	687.9 $\pm$ 40.9a	49.3 $\pm$ 1.0b	0.1326 $\pm$ 0.0031b	1.1417 $\pm$ 0.0035b
50♀: 1♂ (No-choice mating)	306	566.6 $\pm$ 25.1b	52.9 $\pm$ 1.2a	0.1199 $\pm$ 0.0028c	1.1274 $\pm$ 0.0032c

Means followed by the same letter in a column are not significantly different according to the paired bootstrap test at a 5% significance level. The standard errors were estimated using the bootstrap technique with 200,000 resampling.

under laboratory environments are under standardized or artificial conditions. The test insects were well taken care of and supplied with an excess of resources in small containers. Therefore, longer longevity, higher fecundity, and higher population parameters are often observed in the laboratory. This is, by no means, a deficiency of laboratory-generated life tables. It reveals the biological potential of a population under such conditions. However, for practical applications, it is also important to contrast any differences that may occur between life tables obtained under laboratory conditions versus field conditions. Although it is considerably more difficult and many environmental factors cannot be controlled as they are in the laboratory, detecting the differences between laboratory- and field-collected life table data will allow us to produce better applications for both life tables. For example, Raghu and Clarke (2003) showed that the number of matings achieved by methyl-eugenol-fed males was significantly greater than unfed males in small cages

(40 by 40 by 40  $cm^3$ ), but this was not true in larger field cages. The high mating rate observed in our study may be an artifact of the small cage size (15 by 10 by 10  $cm^3$ ), which resulted in an unnatural crowding effect. More studies need to be conducted using larger field cages as shown by Shelly et al (2010). Furthermore, Wong et al. (1991) reported finding significant differences between laboratory-reared and wild-type *D. dorsalis* (i.e., *B. dorsalis* now) in sexual maturation rate and response to methyl eugenol. Matsuyama and Kuba (2009) noticed that the mating times and call frequencies of males may be different between mass-reared and wild strains of the melon fly, *B. cucurbitae* (Coquillett). These reports demonstrate the importance of comparing the critical ecological characteristics of mass-reared versus wild strains. Another important difference between the laboratory and field life tables is that individual rearing is generally practiced in laboratory studies, while in the field, insects may remain in groups during certain stages. This may be especially



**Fig. 5.** (A–D) Population projection showing the numerical increase in different *B. dorsalis* stages during population growth (1F:1M, 1F:50M, 50F:1M-free choice mating, and 50F:1M-no choice mating; F: female, M: male). Because the male (red) and female (green) adult curves are so close together in log scale, their proximity when plotted produces what appears to be a brown line in panel A.

important to fruit flies, because the larvae are able to digest the media more efficiently when reared in a group. To solve the problems occurring in life table data analysis in studies involving group-reared populations, Chang et al. (2016) developed a theory and program to analyze this type of data.

Although sex-ratio manipulation is a promising technique in pest management programs, there remain many aspects that are still little understood and will require additional study before we can fully understand and successfully utilize the strategy to its maximum effect. In this study, we demonstrated that the age-stage, two-sex life table is an essential tool which allows both sexes and the entire life span to be taken into consideration in SIT, and MAT procedures, as well as in other sex ratio manipulation programs.

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## References Cited

Aigaki, T., and S. Ohba. 1984. Effect of mating status on *Drosophila virilis* lifespan. *Exp. Gerontol.* 19: 267–278.

- Alyokhin, A. V., R. H. Messing, and J. J. Duan. 2000. Visual and olfactory stimuli and fruit maturity affect trap captures of oriental fruit flies (Diptera: Tephritidae). *J. Econ. Entomol.* 93: 644–649.
- Alyokhin, A. V., R. H. Messing, and J. J. Duan. 2001. Abundance and mating behavior of oriental fruit flies (Diptera: Tephritidae) near methyl eugenol-baited traps. *Pan Pac. Entomol.* 77: 161–167.
- Arakaki, N., H. Kuba, and H. Soemori. 1984. Mating behavior of the oriental fruit fly, *Dacus dorsalis* Hendel (Diptera: Tephritidae). *Appl. Entomol. Zool.* 19: 42–51.
- Atlihan, R., and H. Chi. 2008. Temperature-dependent development and demography of *Scymnus subvillosus* (Coleoptera: Coccinellidae) reared on *Hyalopecter pruni* (Homoptera: Aphididae). *J. Econ. Entomol.* 101: 325–333.
- Barclay, H. J., and J. Hendrichs. 2014. Models for assessing the male annihilation of *Bactrocera* spp. with methyl eugenol baits. *Ann. Entomol. Soc. Am.* 107: 81–96.
- Barclay, H. J., D. McInnis, and J. Hendrichs. 2014. Modeling the area-wide integration of male annihilation and the simultaneous release of methyl eugenol-exposed *Bactrocera* spp. sterile males. *Ann. Entomol. Soc. Am.* 107: 97–112.
- Bateman, M. A. 1972. The ecology of fruit flies. *Ann. Rev. Entomol.* 17: 493–518.
- Baumhover, A. H., A. J. Graham, D. E. Hopkins, F. H. Dudley, W. D. New, and R. C. Bushland. 1955. Control of screw-worms through release of sterilized flies. *J. Econ. Entomol.* 48: 462–466.
- Benedict, M. Q., and A. S. Robinson. 2003. The first releases of transgenic mosquitoes: an argument for the sterile insect technique. *Trends Parasitol.* 19: 349–355.
- Benelli, G., A. Canale, G. Bonsignori, G. Ragni, C. Stefanini, and A. Raspi. 2012. Male wing vibration in the mating behavior of the olive fruit fly *Bactrocera oleae* (Rossi) (Diptera: Tephritidae). *J. Insect Behav.* 25: 590–603.



- Carey, J. R., P. Liedo, L. Harshman, Y. Zhang, H. G. Müller, L. Partridge, and J. L. Wang. 2002. A mortality cost of virginity at older ages in female Mediterranean fruit flies. *Exp. Gerontol.* 37: 507–512.
- Chi, H. 1988. Life-table analysis incorporating both sexes and variable development rates among individuals. *Environ. Entomol.* 17: 26–34.
- Chi, H. 1990. Timing of control based on the stage structure of pest populations: a simulation approach. *J. Econ. Entomol.* 83: 1143–1150.
- Chi, H. 2016a. TIMING-MSChart: a computer program for the population projection based on age-stage, two-sex life table. National Chung Hsing University, Taichung, Taiwan. (<http://140.120.197.173/Ecology/Download/Timing-MSChart.zip>) (accessed 1 May 2016).
- Chi, H. 2016b. TWSEX-MSChart: a computer program for the age-stage, two-sex life table analysis. National Chung Hsing University, Taichung, Taiwan. (<http://140.120.197.173/Ecology/Download/Twosex-MSChart.zip>) (accessed 1 May 2016).
- Chi, H., and H. Liu. 1985. Two new methods for the study of insect population ecology. *Bull. Inst. Zool. Acad. Sin.* 24: 225–240.
- Chi, H., and Y. Su. 2006. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. *Environ. Entomol.* 35: 10–21.
- Chiu, H. T., and Y. I. Chu. 1988. The male annihilation of Oriental fruit fly on Lambay Island. *Chin. J. Entomol.* 8: 81–94.
- Chu, Y. I., and H. T. Chiu. 1989. The re-establishment of *Dacus dorsalis* Hendel (Diptera: Tephritidae) after the eradication on Lambay Island. *Chin. J. Entomol.* 9: 217–230.
- Chang, C., C. Y. Huang, S. M. Dai, R. Atlihan, and H. Chi. 2016. Genetically engineered ricin suppresses *Bactrocera dorsalis* (Diptera: Tephritidae) based on demographic analysis of group-reared life table. *J. Econ. Entomol.* 109: 987–992.
- Cornelius, M. L., L. Nergel, J. J. Duan, and R. H. Messing. 2000. Responses of female oriental fruit flies (Diptera: Tephritidae) to protein and host fruit odors in field cage and open field tests. *Environ. Entomol.* 29: 14–19.
- Cunningham, R. T., and D. Y. Suda. 1986. Male annihilation through mass-trapping of male flies with methyleugenol to reduce infestation of Oriental fruit fly (Diptera: Tephritidae) larvae in papaya. *J. Econ. Entomol.* 79: 1580–1582.
- Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman & Hall, New York, NY.
- Fanson, B. G., K. V. Fanson, and P. W. Taylor. 2012. Cost of reproduction in the Queensland fruit fly: Y-model versus lethal protein hypothesis. *Proc. R. Soc. B* 279: 4893–4900.
- Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.
- Gabre, R. B., F. K. Adham, and H. Chi. 2005. Life table of *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae). *Acta Oecologica* 21: 179–183.
- Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. *Am. Nat.* 119: 803–823.
- Hendrichs, J., P. Kenmore, A. S. Robinson, and M. J. B. Vreysen. 2007. Area-wide integrated pest management (AW-IPM): principles, practice and prospects, pp. 3–33. In M. J. B. Vreysen, A. S. Robinson and J. Hendrichs (eds.), Area-wide control of insect pests: from research to field implementation. Springer, Dordrecht, Netherlands.
- Hornig, S. B., and R. E. Plant. 1993. Lek mating system and its impact on male annihilation technique. *Res. Popul. Ecol.* 35: 183–197.
- Huang, Y. B., and H. Chi. 2012a. 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. *Insect Sci.* 19: 803–823.
- Huang, Y. B., and H. Chi. 2012b. Assessing the application of the jackknife and bootstrap techniques to the estimation of the variability of the net reproductive rate and gross reproductive rate: a case study in *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae). *J. Agric. For.* 61: 37–45.
- Huang, Y. B., and H. Chi. 2013. Life tables of *Bactrocera cucurbitae* (Diptera: Tephritidae): with an invalidation of the jackknife technique. *J. Appl. Entomol.* 137: 327–339.
- Huang, Y. B. K., and H. Chi. 2014. Fitness of *Bactrocera dorsalis* (Hendel) on seven host plants and an artificial diet. *Turk. Entomol. Derg.* 38: 401–414.
- Iwahashi, O., and T. Majima. 1986. Lek formation and male-male competition in the melon fly, *Dacus cucurbitae* Coquillett (Diptera: Tephritidae). *Appl. Entomol. Zool.* 21: 70–75.
- Jang, E. B., and D. M. Light. 1991. Behavioral responses of female oriental fruit flies to the odor of papayas at three ripeness stages in a laboratory flight tunnel (Diptera: Tephritidae). *J. Insect Behav.* 4: 751–762.
- Knipling, E. F. 1955. Possibilities of insect control or eradication through the use of sexually sterile males. *J. Econ. Entomol.* 48: 459–462.
- Knipling, E. F. 1985. Sterile insect technique as a screwworm control measure. The concept and its development. *Miscellaneous Publ. Entomol. Soc. Am.* 62: 8–11.
- Lance, D. R., and D. O. McInnis. 2005. Biological basis of the sterile insect technique, pp. 69–94. In V. A. Dyck, J. Hendrichs and A. S. Robinson (eds.), Sterile insect technique: principles and practice in area-wide integrated pest management. Springer, Dordrecht, The Netherlands.
- Lee, W. Y. 1988. The control programme of the Oriental fruit fly in Taiwan. *Chin. J. Entomol.* 2: 51–60.
- Leftwich, P. T., D. A. Edward, L. Alphey, M. J. G. Gage, and T. Chapman. 2012. Variation in adult sex ratio alters the association between courtship, mating frequency and paternity in the lek-forming fruitfly *Ceratitis capitata*. *J. Evol. Biol.* 25: 1732–1740.
- Lewontin, R. C. 1965. Selection for colonizing ability. The Genetics of Colonizing Species (eds. H. G. Baker and G. L. Stebbins.) pp. 77–94. Academic Press, San Diego, CA.
- Matsuyama, T., and H. Kubo. 2009. Mating time and call frequency of males between mass-reared and wild strains of melon fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae). *Appl. Entomol. Zool.* 44: 309–314.
- Meats, A., P. Maheswaran, M. Frommer, J. Sved. 2002. Towards a male-only release system for SIT with the Queensland fruit fly, *Bactrocera tryoni*, using a genetic sexing strain with a temperature-sensitive lethal mutation. *Genetica* 116: 97–106.
- Miyatake, T., and D. Haraguchi. 1996. Mating success in *Bactrocera cucurbitae* (Diptera: Tephritidae) under different rearing densities. *Ann. Entomol. Soc. Am.* 89: 284–289.
- Mou, D. F., C. C. Lee, C. L. Smith, and H. Chi. 2015. Using viable eggs to accurately determine the demographic and predation potential of *Harmonia dimidiata* (Coleoptera: Coccinellidae). *J. Appl. Entomol.* 139: 579–591.
- Muhammad, S. 2015. Field tests for exploiting the behavioral control tactics to pest Tephritid fruit flies (Insecta: Diptera). *Int. J. Anim. Biol.* 1: 243–248.
- Papadopoulos, N. T., P. Liedo, H. G. Müller, J. L. Wang, F. Molleman, and J. R. Carey. 2010. Cost of reproduction in male medflies: The primacy of sexual courting in extreme longevity reduction. *J. Insect Physiol.* 56: 283–287.
- Pereira, R., B. Yuval, P. Liedo, P. E. A. Teal, T. E. Shelly, D. O. McInnis, and J. Hendrichs. 2013. Improving sterile male performance in support of programmes integrating the sterile insect technique against fruit flies. *J. Appl. Entomol.* 137: 178–190.
- Polat-Akköprü, E., R. Atlihan, H. Okut, and H. Chi. 2015. Demographic assessment of plant cultivar resistance to insect pests: a case study of the dusky-veined walnut aphid (Hemiptera: Callaphididae) on five walnut cultivars. *J. Econ. Entomol.* 108: 378–387.
- Raghu, S., and A. R. Clarke. 2003. Sexual selection in a tropical fruit fly: role of a plant derived chemical in mate choice. *Entomol. Exp. Appl.* 108: 53–58.
- Robinson, A. S. 1983. Sex-ratio manipulation in relation to insect pest control. *Ann. Rev. Genet.* 17: 191–214.
- Saadat, D., A. A. Seraj, S. H. Goldansaz, and L. Williams, III. 2016. Factors affecting reproductive success and life history parameters of *Bracon hebetor* Say (Hymenoptera: Braconidae) from three host-associated populations. *Biol. Control* 96: 86–92.
- Shelly, T. E., and E. M. Villalobos. 2004. Host plant influence on the mating success of male Mediterranean fruit flies: variable effects within and between individual plants. *Anim. Behav.* 68: 417–426.
- Shelly, T. E., D. O. McInnis, C. Rodd, J. Edu, and E. Paho. 2007. Sterile insect technique and Mediterranean fruit fly (Diptera: Tephritidae): assessing the utility of aromatherapy in a Hawaiian coffee field. *J. Econ. Entomol.* 100: 273–282.

- Shelly, T. E., J. Edu, D. McInnis. 2010. Pre-release consumption of methyl eugenol increases the mating competitiveness of sterile males of the Oriental fruit fly, *Bactrocera dorsalis*, in large field enclosures. *Journal of Insect Science*. 10: 1–16.
- Steiner, L. F. 1952. Methyl eugenol as an attractant for oriental fruit fly. *J. Econ. Entomol.* 63: 241–248.
- Steiner, L. F., W. C. Mitchell, E. J. Harris, T. T. Kozuma, and M. S. Fujimoto. 1965. Oriental fruit fly eradication by male annihilation. *J. Econ. Entomol.* 58: 961–964.
- Tuan, S. J., C. C. Lee, and H. Chi. 2014a. Population and damage projection of *Spodoptera litura* (F.) on peanuts (*Arachis hypogaea* L.) under different conditions using the age-stage, two-sex life table. *Pest Manag. Sci.* 70: 805–813.
- Tuan, S. J., C. C. Lee, and H. Chi. 2014b. Population and damage projection of *Spodoptera litura* (F.) on peanuts (*Arachis hypogaea* L.) under different conditions using the age-stage, two-sex life table. *Pest Manag. Sci.* 70: 1936.
- Tuan, S. J., C. C. Yeh, R. Atlihan, and H. Chi. 2016. Linking life table and predation rate for biological control: a comparative study of *Eocantbecona furellata* (Hemiptera: Pentatomidae) fed on *Spodoptera litura* (Lepidoptera: Noctuidae) and *Plutella xylostella* (Lepidoptera: Plutellidae). *J. Econ. Entomol.* 109: 13–24.
- Vargas, R. I., R.F.L. Mau, E. B. Jang, R. M. Faust, and L. Wong. 2008. The Hawaii fruit fly areawide pest management programme, pp. 300–325. *In* O. Koul, G. Cuperus and N. Elliott (eds.), *Areawide pest management: theory and implementation*. CAB International, Wallingford, United Kingdom.
- Vargas, R. I., W. A. Walsh, E. B. Jang, J. W. Armstrong, and D. T. Kanehisa. 1996. Survival and development of immature stage of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. *Ann. Entomol. Soc. Am.* 89: 64–69.
- Vargas, R. I., W. A. Walsh, D. Kanehisa, E. B. Jang, and J. W. Armstrong. 1997. Demography of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. *Ann. Entomol. Soc. Am.* 90: 162–168.
- Vargas, R. I., W. A. Walsh, D. Kanehisa, J. D. Stark, and T. Nishida. 2000. Comparative demography of three Hawaiian fruit flies (Diptera: Tephritidae) at alternating temperatures. *Ann. Entomol. Soc. Am.* 93: 75–81.
- Vargas-Terán, M., H. C. Hofmann, and N. E. Tweddle. 2005. Impact of screwworm eradication programmes using the sterile insect technique, pp. 629–650. *In* V. A. Dyck, J. Hendrichs and A. S. Robinson (eds.), *Sterile insect technique: principles and practice in area-wide integrated pest management*. Springer, Dordrecht, The Netherlands.
- Vreysen, M.J.B., M. Khalfan, M. Saleh, M. Y. Ali, M. Abdulla, Z. R. Zhu, K. G. Juma, A. R. Msangi, P. A. Mkonyi, et al. 2000. *Glossina austeni* (Diptera: Glossinidae) eradicated on the Island of Unguja, Zanzibar, using the sterile insect technique. *J. Econ. Entomol.* 93: 123–135.
- Vreysen, M.J.B. 2001. Principles of area-wide integrated tsetse fly control using the sterile insect technique. *Med. Trop.* 61: 397–411.
- White, I. M., and M. M. Elson-Harris. 1992. *Fruit flies of economic significance: their identification and bionomics*. CAB International, Wallingford, Oxon, United Kingdom, 601 pp.
- Wong, T.T.Y., D. O. McInnis, and J. I. Nishimoto. 1989. Relationship of sexual maturation rate to response of oriental fruit fly strains (Diptera: Tephritidae) to methyl eugenol. *J. Chem. Ecol.* 15: 1399–1405.
- Wong, T.T.Y., D. O. McInnis, M. M. Ramadan, and J. I. Nishimoto. 1991. Age-related response of male melon flies *Dacus cucurbitae* (Diptera: Tephritidae) to cue-lure. *J. Chem. Ecol.* 17: 2481–2487.
- Yang, P. J., J. R. Carey, and R. V. Dowell. 1994. Temperature influences on the development and demography of *Bactrocera dorsalis* (Diptera: Tephritidae) in China. *Environ. Entomol.* 23: 971–974.