

**Orijinal araştırma (Original article)**

**Fitness of *Bactrocera dorsalis* (Hendel) on seven host plants  
and an artificial diet**

*Bactrocera dorsalis* (Hendel)'in yedi konukçu bitki ve bir yapay besin  
üzerindeki performansı

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**Summary**

The oriental fruit fly, *Bactrocera dorsalis* (Hendel), is one of the most destructive pests in the Asia and Pacific area and is an important quarantine pest for the United States and many countries. This fly attacks more than 150 cultivated and wild fruits in Taiwan. To build an ecological database, we studied the life tables of *B. dorsalis* reared on seven host plants and an artificial diet at 25±1°C, 70±10% R.H., and a photoperiod of 12:12 (L:D) h. The life history raw data were analyzed using an age-stage, two-sex life table. The mean fecundity ( $F$ ) ranged from 252.3 to 1300.3 eggs per female, and the highest fecundity was observed on pomelo; the net reproductive rate ( $R_0$ ) ranged from 100.9 to 588.3, and the highest reproductive rate was observed on jujube. The intrinsic rate of increase ( $r$ ) was 0.1790, 0.1667, 0.1333, 0.1261, 0.1161, 0.1128, 0.1120, and 0.0797d<sup>-1</sup> on pitaya, artificial diet, guava, sweet orange, wax apple, pomelo, jujube, and wild-type mango in descending order, respectively. The high fecundity, net reproductive rates, and intrinsic rates of increase on these common fruits explain not only the high fitness of *B. dorsalis* as a pest in many areas but also the difficulty in managing this pest in past decades, as well. Finally, the results of a population projection could reveal the population growth and stage structure. The study were demonstrated that the age-stage, two-sex life table is a promising and reliable tool for pest management and general ecological study.

**Keywords:** *Bactrocera dorsalis*, life table, host plant

**Özet**

Doğu meyve sineği, *Bactrocera dorsalis* (Hendel) Asya ve Pasifik bölgesinde ana zararlılardan biri, Amerika Birleşik Devletleri başta olmak üzere pek çok ülkede de önemli bir karantina zararlısıdır. Bu zararlı Tayvan'da 150'den fazla kültür bitkisine saldırmaktadır. Bu çalışmada zararlıya ilişkin ekolojik temel bazı bilgilerin elde edilmesi için yedi farklı konukçu bitki ve bir yapay besin üzerinde zararlının yaşam çizelgesi parametreleri elde edilmiştir. Çalışma, 25±1°C sıcaklık, %70±10 orantılı nem ve 12:12 saatlik aydınlık-karanlık koşullarını sağlayan iklim odasında yürütülmüştür. Elde edilen veriler iki eşeyli yaş ve döneme bağlı yaşam çizelgesine göre analiz edilmiştir. Çalışmada elde edilen sonuçlara göre, bırakılan ortalama yumurta sayısı 252.3 ile 1300.3 arasında değişmiş olup, en yüksek değer pomelo üzerinde elde edilmiştir. Net üreme gücü ( $R_0$ ) değeri konukçu bitkiye bağlı olarak 100.9 ile 588.3 arasında değişiklik göstermiş ve en yüksek olarak jujube üzerinde elde edilmiştir. Kalıtsal üreme yeteneği ( $r$ ) pitaya, yapay besin, guava, tatlı portakal, balmumu elma (wax apple), pomelo, jujube ve yabani tip mango üzerinde sırasıyla 0.1790, 0.1667, 0.1333, 0.1261, 0.1161, 0.1128, 0.1120, ve 0.0797g<sup>-1</sup> olarak bulunmuştur. Bu çalışmada kullanılan ve yaygın olarak bulunan meyveler üzerinde elde edilen yüksek doğurganlık, net üreme gücü ve kalıtsal üreme yeteneği değerleri, son yıllarda bu zararlıyı kontrol etmenin neden güç olduğunu açıklamaktadır. Elde edilen sonuçlar popülasyonun dönem yapısı ve gelişmesine ilişkin önemli bilgiler sunmakta, iki eşeyli yaş ve döneme bağlı yaşam çizelgesinin ekolojik çalışmalar ve zararlı yönetim programlarında yararlanılabilecek önemli bir araç olduğunu göstermektedir.

**Anahtar sözcükler:** *Bactrocera dorsalis*, yaşam çizelgesi, konukçu bitki

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## Introduction

The oriental fruit fly, *Bactrocera dorsalis* (Hendel), is one of the most destructive pests of fruit crops in the Asia-Pacific area and the most important quarantine pest for many countries, including European countries and the United States (CABI & EPPO, 1997). This fly attacks more than 150 cultivated and wild fruits in Taiwan; among the cultivated fruits, twenty economically important fruits are widely planted on approximately 190,000 ha of orchards (Agriculture & Food Agency, 2013). In Taiwan, although a huge amount of government funding has been continuously allocated for the control of this pest in the last five decades, it remains at the top of the major pest list.

For the construction of an ecological-oriented management program for a pest such as *B. dorsalis*, with a wide host plant range and distribution, a complete database of pest ecology on major hosts is very important and urgently needed. Among all the ecological data, life tables offer the most comprehensive description of the survival, stage differentiation, and reproduction of pest populations. The importance of life table data has been repeatedly noted in many reviews (Bateman, 1972; Carey, 2001), and life tables of various pests have been reported as well (e.g., Carey et al., 1988, Vargas & Carey, 1990; Vargas et al., 1997; Vargas et al., 2000; Legaspi et al., 2011), based on traditional female age-specific life tables (Lewis, 1942; Leslie, 1945; Birch, 1948). Because the female age-specific life tables ignore stage differentiation and the male population, Huang & Chi (2012a) listed the problems of applying those life tables to insect populations. To overcome the shortcomings of traditional female age-specific life tables, Chi & Liu (1985) and Chi (1988) developed the age-stage, two-sex life table to correctly describe the survival, development, stage differentiation, and reproduction of a two-sex population, and it has been applied to many economically important pest species and biological control agents (e.g., Guo et al., 2012; Muştu & Kılınçer, 2013; Núñez-Campero et al., 2014).

Because most insects spend their whole life on a single host plant or two, the host plant plays an important role on their development, survival, and fecundity, and life table studies on the major host plants are critically important for the construction of an ecological database (Vargas et al., 1990). In this study, seven major fruit plants (mango, guava, jujube, wax apple, sweet orange, pomelo, and pitaya) and an artificial diet were selected for the study of the life table of *B. dorsalis*, and all raw data were analyzed by using the age-stage, two-sex life table to correctly describe the stage differentiation while including both sexes. These data can be used in an area-wide management of *B. dorsalis*, where different host plants are cultivated.

## Materials and Methods

### Insects

Wild-caught *B. dorsalis* were originally collected near Wufeng County in 1996 and have since been mass reared for more than 200 generations in the insectary of the Agriculture Research Institute, Wufeng, Taichung, Taiwan. Larvae were reared on an artificial diet with modified composition according to Tanaka *et al.* (1969). The composition of the diet was sodium benzoate 5 g, granulated sugar 240 g, yeast 140 g, HCl 20 ml, wheat shorts 480 g, and water 1100 ml. Adults were reared on a mixture of sucrose, yeast extract and water (1:5:0.25). Flies were kept in a growth chamber at  $25 \pm 1^\circ\text{C}$ ,  $70 \pm 10\%$  RH, and at a photoperiod of 12:12 (L:D) h. The survival rate, fecundity, and hatch rate were regularly monitored and compared with the wild population to assure that no degeneration occurred.

### Host plants

Fruits of seven host plants were used in this study. They were guava (pearl strain, *Psidium guajava* Linn.), jujube (Indian jujube, *Zizyphus mauritiana* Linn.), wax apple (black pearl, *Syzygium samarangense* Merr. & Perry), pomelo (*Citrus grandis* Osbeck), sweet orange (*Citrus sinensis* (Linn.) Osbeck), pitaya (*Hylocereus* spp. Britt. & Rose), and wild-type mango ("Jin-Huang", *Mangifera indica* Linn.). Fruits were obtained from the experimental field of the Taiwan Agriculture Research Institute, Taichung, Taiwan.

### Life table study

Before the life table study, newly emerged adults were first collected from the mass rearing colony and paired in cages (15×15×60 cm) with adult food and fresh fruit slices (approximately 0.2 cm thick) of the respective host plants for oviposition. After two generations, 100 eggs laid within 24 h were collected for the life table study. Eggs were maintained separately in individual cages.

During the egg and larval stage, insects were checked with a microscope (Leica MZ 9) to record the egg hatch and the survival of the larvae until pupation. Fruit slices were replaced every 2-3 d with fresh fruit slices as necessary. After adult emergence, individuals were paired and transferred to a new cage with adult food. For the collection of daily egg production, fresh fruit slices were placed in each cage and renewed daily. The fecundity and survival of adults were recorded daily until the death of all individuals.

### Life table analysis

The age-stage specific survival rate ( $s_{xj}$ , where  $x$ =age in d and  $j$ =stage), age-stage specific fecundity ( $f_{xj}$ ), age-specific survival rate ( $l_x$ ), the age-specific fecundity ( $m_x$ ) were calculated according to the age-stage, two-sex life table theory (Chi & Liu, 1985; Chi, 1988). The  $l_x$  and  $m_x$  are calculated as follows:

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

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

where  $k$  is the number of stages and  $s_{xj}$  is the probability a newly laid egg will survive to age  $x$  and stage  $j$ . The adult preoviposition period (APOP, the duration from female adult emergence to the first oviposition) and the total preoviposition period (TPOP, the duration from birth to the first oviposition age) were calculated from the raw data of an individual female. The population parameters were estimated in sequence; they are the net reproductive rate ( $R_0$ ), the intrinsic rate of increase ( $r$ ), the finite rate of increase ( $\lambda$ ), and the mean generation time ( $T$ ). The net reproductive rate is calculated as

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

The intrinsic rate of increase is estimated using the iterative bisection method from the Euler-Lotka formula with the age indexed from 0 (Goodman, 1982).

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

The finite rate ( $\lambda$ ) is calculated as  $\lambda = e^r$ . The mean generation time 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 ( $e_{xj}$ ) was calculated according to Chi & Su (2006) as

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

where  $s'_{iy}$  is the probability that individuals of age  $x$  and stage  $j$  will survive to age  $i$  and stage  $y$  and is calculated by assuming  $s'_{xj} = 1$ . The reproductive value ( $v_{xj}$ ) was calculated according to Tuan et al. (2014) and is calculated 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 TWSEX-MS Chart (Chi, 2013) was used in this analysis. The program is written in Visual BASIC for the Windows operating system and is available at <http://140.120.197.173/Ecology/Download/Twosex.rar>. For the estimation of the standard errors of developmental time, longevity, fecundity, and population parameters, the bootstrap technique (Efron & Tibshirani, 1993; Huang & Chi, 2012b; Huang & Chi, 2013; Polat Akköprü et al. 2015) was used with 40,000 bootstraps. We then used the paired bootstrap test (Efron & Tibshirani, 1993) to compare the differences from the bootstrap results of all treatments. The bootstrap procedures and paired bootstrap test were embedded in the TWSEX-MS Chart.

### Population projection

The life table data collected on the seven fruits and the artificial diet were used to project the population growth based on the method of Chi & Liu (1985) and Chi (1990) by using the computer program TIMING-MSChart (Chi, 2014), which is also available at <http://140.120.197.173/Ecology/>.

## Results

The developmental time of each stage, adult longevity, and fecundity of *B. dorsalis* are shown in Table 1. There were various differences in the development time of egg, larval, and pupal stages among treatments. The preadult duration ranged from 16.27 d (reared on pitaya) to 24.0 d (on mango). Male adult longevity ranged from 45.5d (on pitaya) to 116.5 d (on pomelo), while female longevity ranged from 55.2 d (on pitaya) to 125.1 d (on jujube). When larvae were reared on sweet orange, guava, pomelo, or jujube, both female and male adults could survive longer than three months. The stage differentiation and survival rate ( $s_{xj}$ ) of *B. dorsalis* reared on different media are shown in Fig. 1. Because the two-sex life table takes the variable developmental rate among individuals into consideration, the stage overlapping can be observed in the curves of the  $s_{xj}$ .

The lifetime fecundity per female ( $F$ ) ranged from 252.3 eggs (on mango) to a very high value of 1300.3 eggs (on pomelo) (Table 1). The difference in daily fecundities among host plants can be observed in the curve of the age-specific fecundity ( $m_x$ ) (Fig. 2). When the fruit flies were reared on mango or wax apple, the  $m_x$  curves were low (mostly less than 10 eggs per day), while most flies reared on pomelo could lay more than 10 eggs daily and lasted for a long period (> 200 d). The age-specific fecundity ( $m_x$ ) and maternity ( $l_x m_x$ ) showed a decreasing trend with age (Fig. 2). Higher age-specific daily fecundities of the female ( $m_x = 10 - 30$  eggs) were observed during ages 25-45 d for fruit flies on the mango and the artificial diet. Although fruit flies reared on pomelo showed a peak of fecundity at the end of their lives, due to the low survival rate at the end of life, the contribution of those eggs to the net reproductive rate was minor.

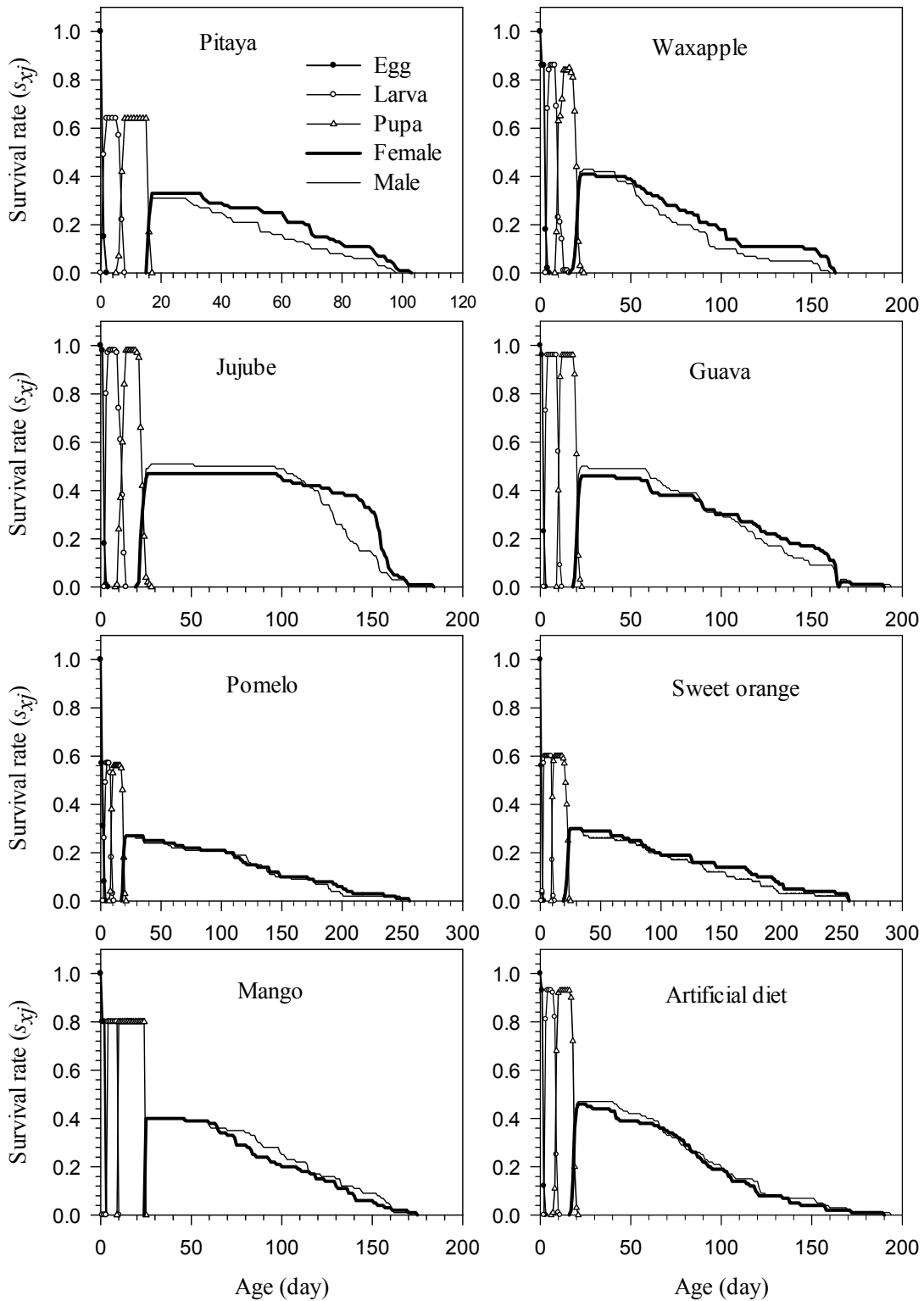


Fig. 1. Age-stage specific survivorship of *Bactrocera dorsalis* on various host plants.

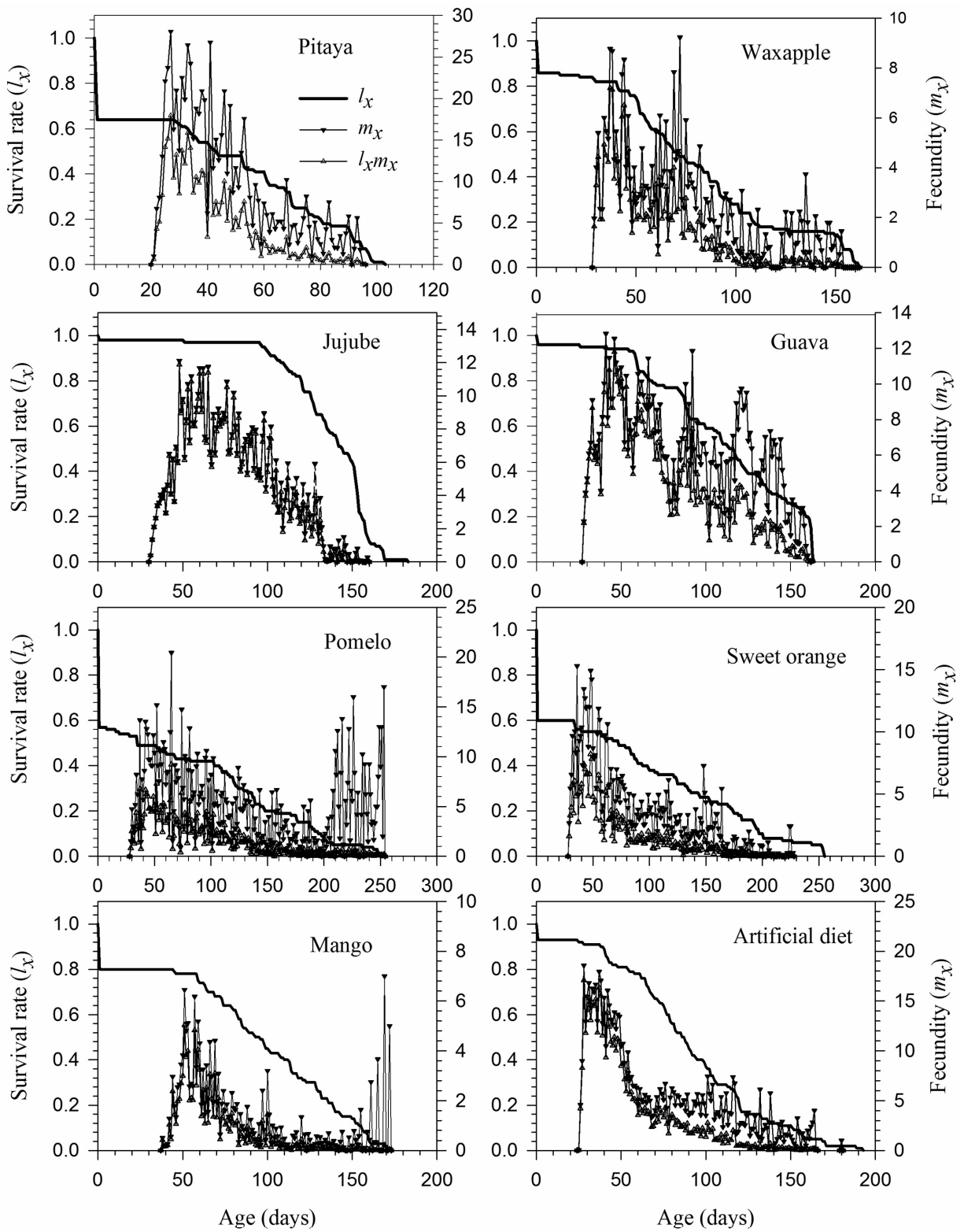


Fig. 2. Age-specific survival rate ( $l_x$ ), age-specific fecundity ( $m_x$ ), and age-specific maternity ( $l_x m_x$ ) of *Bactrocera dorsalis* reared on different media.

Table 1. Development periods (d) (mean  $\pm$  SE) of *B. dorsalis* reared on different media at 25°C. Standard errors were estimated by using bootstrap method with 40,000 bootstraps

Host plant	Pitaya	Sweet orange	Guava	Pomelo	Waxapple	Jujube	Mango	Artificial diet
Egg	1.23 $\pm$ 0.05f	1.98 $\pm$ 0.04e	2.24 $\pm$ 0.04d	2.68 $\pm$ 0.09c	3.23 $\pm$ 0.05a	2.19 $\pm$ 0.04d	3.00 $\pm$ 0.00b	2.13 $\pm$ 0.03d
Larva	6.00 $\pm$ 0.08d	7.33 $\pm$ 0.07b	7.44 $\pm$ 0.05b	5.61 $\pm$ 0.10e	6.28 $\pm$ 0.13c	8.70 $\pm$ 0.14a	6.00 $\pm$ 0.00d	6.02 $\pm$ 0.06d
Pupa	9.03 $\pm$ 0.08e	12.53 $\pm$ 0.16b	9.98 $\pm$ 0.07d	9.89 $\pm$ 0.10d	9.94 $\pm$ 0.14d	11.45 $\pm$ 0.14c	15.00 $\pm$ 0.00a	9.84 $\pm$ 0.09d
Preadult	16.27 $\pm$ 0.06h	21.85 $\pm$ 0.17c	19.66 $\pm$ 0.09d	18.2 $\pm$ 0.11f	19.44 $\pm$ 0.13e	22.35 $\pm$ 0.14b	24.00 $\pm$ 0.00a	17.99 $\pm$ 0.08g
Fecundity ( <i>F</i> ) (eggs)	1082.5 $\pm$ 115.9a	1024.6 $\pm$ 139.8a	1257.7 $\pm$ 112.1a	1300.3 $\pm$ 178.6a	425.0 $\pm$ 63.8b	1251.6 $\pm$ 76.3a	252.3 $\pm$ 33.5b	1122.0 $\pm$ 123.5a
Adult female	55.2 $\pm$ 3.7dA	124.6 $\pm$ 11.8aA	100.2 $\pm$ 5.7bA	122.2 $\pm$ 12.0aA	79.3 $\pm$ 6.2cA	125.1 $\pm$ 2.8aA	82.3 $\pm$ 5.5cA	75.0 $\pm$ 5.5cA
Adult male	45.5 $\pm$ 3.9dB	108.8 $\pm$ 11.5aB	91.3 $\pm$ 5.1bB	116.5 $\pm$ 11.7aA	60.9 $\pm$ 5.4cB	109.5 $\pm$ 3.0aB	90.1 $\pm$ 5.3bB	78.3 $\pm$ 5.5bB

Means followed by a different lowercase letter within each row are significantly different among treatments ( $P < 0.05$ , paired bootstrap test.) Means followed by a different uppercase letter denote a significant difference in adult longevity between female and male.

Table 2. Population parameters (mean  $\pm$  SE) of *B. dorsalis* reared on various media at 25°C (APOP, adult preoviposition period; TPOP, total preoviposition period;  $N_f$ , number of females emerged from 100 eggs;  $r$ , intrinsic rate of increase;  $\lambda$ , finite rate;  $R_0$ , net reproductive rate; and  $T$ , mean generation time)

Diet	Pitaya	Sweet orange	Guava	Pomelo	Waxapple	Jujube	Mango	Artificial diet
APOP (d)	7.52 $\pm$ 0.32d	8.37 $\pm$ 0.41d	12.09 $\pm$ 0.49c	16.12 $\pm$ 0.81b	13.70 $\pm$ 0.78bc	12.47 $\pm$ 0.52c	20.48 $\pm$ 0.72a	10.98 $\pm$ 0.75c
TPOP (d)	23.82 $\pm$ 0.32e	30.33 $\pm$ 0.35cd	31.83 $\pm$ 0.51bc	34.24 $\pm$ 0.79b	33.17 $\pm$ 0.75b	34.53 $\pm$ 0.52b	44.48 $\pm$ 0.72a	28.89 $\pm$ 0.75d
Females ( $N_f$ )	33 $\pm$ 4.7bcd	30 $\pm$ 4.7cd	46 $\pm$ 5.0ab	27 $\pm$ 4.5d	41 $\pm$ 5.0ac	47 $\pm$ 5.0a	40 $\pm$ 4.9ad	46 $\pm$ 5.0a
$R_0$ (eggs)	357.2 $\pm$ 63.4b	307.4 $\pm$ 62.6b	578.6 $\pm$ 81.0a	351.1 $\pm$ 74.6b	174.3 $\pm$ 33.2c	588.3 $\pm$ 72.7a	100.9 $\pm$ 18.1c	516.1 $\pm$ 79.4a
$T$ (d)	32.83 $\pm$ 0.63f	45.44 $\pm$ 0.92d	47.71 $\pm$ 1.09c	52.33 $\pm$ 1.43b	44.45 $\pm$ 0.91d	56.53 $\pm$ 0.86a	57.88 $\pm$ 1.46a	37.48 $\pm$ 0.58e
$r$ (d <sup>-1</sup> )	0.1790 $\pm$ 0.0063a	0.1261 $\pm$ 0.0054c	0.1333 $\pm$ 0.0041c	0.1120 $\pm$ 0.0056d	0.1161 $\pm$ 0.0052d	0.1128 $\pm$ 0.0032d	0.0797 $\pm$ 0.0039e	0.1667 $\pm$ 0.0048b
$\lambda$ (d <sup>-1</sup> )	1.1961 $\pm$ 0.0075a	1.1344 $\pm$ 0.0061c	1.1426 $\pm$ 0.0047c	1.1185 $\pm$ 0.0062d	1.1231 $\pm$ 0.0058d	1.1194 $\pm$ 0.0036d	1.0830 $\pm$ 0.0042e	1.1814 $\pm$ 0.0056b

Means followed by the same letter in a row are not significantly different ( $P > 0.05$ , paired bootstrap test).

The effect of the host plant on the development of *B. dorsalis* can also be observed in the adult preoviposition period (APOP) and the total preoviposition period (TPOP). The shortest APOP (7.52 d) and TPOP (23.82 d) were observed on pitaya, while the longest APOP (20.48 d) and TPOP (44.48 d) were observed on mango (Table 2). When reared on pomelo, the numbers of emerged female adults ( $N_f$ ) were significantly lower than with other treatments, except no difference in the  $N_f$  was observed with sweet orange. The highest intrinsic rate of increase ( $r = 0.1790 \text{ d}^{-1}$ ) and finite rate ( $\lambda = 1.1961 \text{ d}^{-1}$ ) were observed on pitaya, while the lowest  $r$  (0.0797) and  $\lambda$  (1.0830  $\text{d}^{-1}$ ) were observed on wild mango. The highest net reproductive rates ( $R_0$ ) were, however, observed on guava, jujube, and artificial diet, i.e., 578.6, 588.3 and 516.1, respectively, and these rates were significantly higher than with the other five treatments. The shortest mean generation time ( $T$ ) was 32.83 d on pitaya, and this was significantly shorter than that of the other seven treatments.

The age-stage specific life expectancy ( $e_{xj}$ ) (Fig. 3) showed the differences in the time length that individuals of age  $x$  and stage  $j$  were expected to live in different treatments. The life expectancy of a newly laid egg ( $e_{01}$ ) was 43.09, 83.53, 110.64, 75.12, 76.09, 136.55, 88.32, and 88.14 on pitaya, sweet orange, guava, pomelo, wax apple, jujube, wild mango, and artificial diet, respectively. Because there were mortalities in the egg stage in most treatments, the life expectancy of eggs was, in general, shorter than that of the larvae (Fig. 3). In all treatments, the newly hatched larvae had the highest life expectancies; these were 65.77, 137.55, 113.21, 129.04, 85.31, 137.32, 107.15, and 92.7 d on pitaya, sweet orange, guava, pomelo, wax apple, jujube, wild mango, and artificial diet, respectively. There were, however, no significant differences between male and female adults, in general, except on the pomelo, where male adults had a longer life expectancy than females. Because the survival rate of individuals in the laboratory was mainly affected by aging, the life expectancy decreased gradually with age from the larval stage onward in all treatments.

The reproductive value ( $v_{xj}$ ) (Fig. 4) shows the contribution of individuals at age  $x$  and stage  $j$  of the oriental fruit fly to the future population (Fisher, 1930). The reproductive value for a newly laid egg ( $v_{01}$ ) is exactly the finite rate of increase; for example, the  $v_{01}$  of *B. dorsalis* reared on pitaya is exactly its finite rate 1.1961 (Table 2). The reproductive value significantly increased at the age of emergence of the adult females and the beginning of reproduction. For example, the  $v_{xj}$  of *B. dorsalis* reared on pitaya jumped to 63.58 at age 16 d when female adults emerged. The  $v_{xj}$  jumped then to 155.63 at age 21 d when the females began to lay eggs. It increased again to a peak of  $v_{xj}$  (239.54) at age 25 d when most females began to lay eggs, which is close to the mean of the TPOP (23.8 d).

The population growth for each treatment projected with an initial population of ten eggs was shown in Fig. 5. Because *B. dorsalis* grew very fast, the population increased more than 100 to 1000-fold and must be shown in logarithmic scale to make the initial population visible. The scale showed that *B. dorsalis* grows much faster on pitaya and artificial diet than on other treatments. The emergence time of each stage could be observed in Fig. 5.



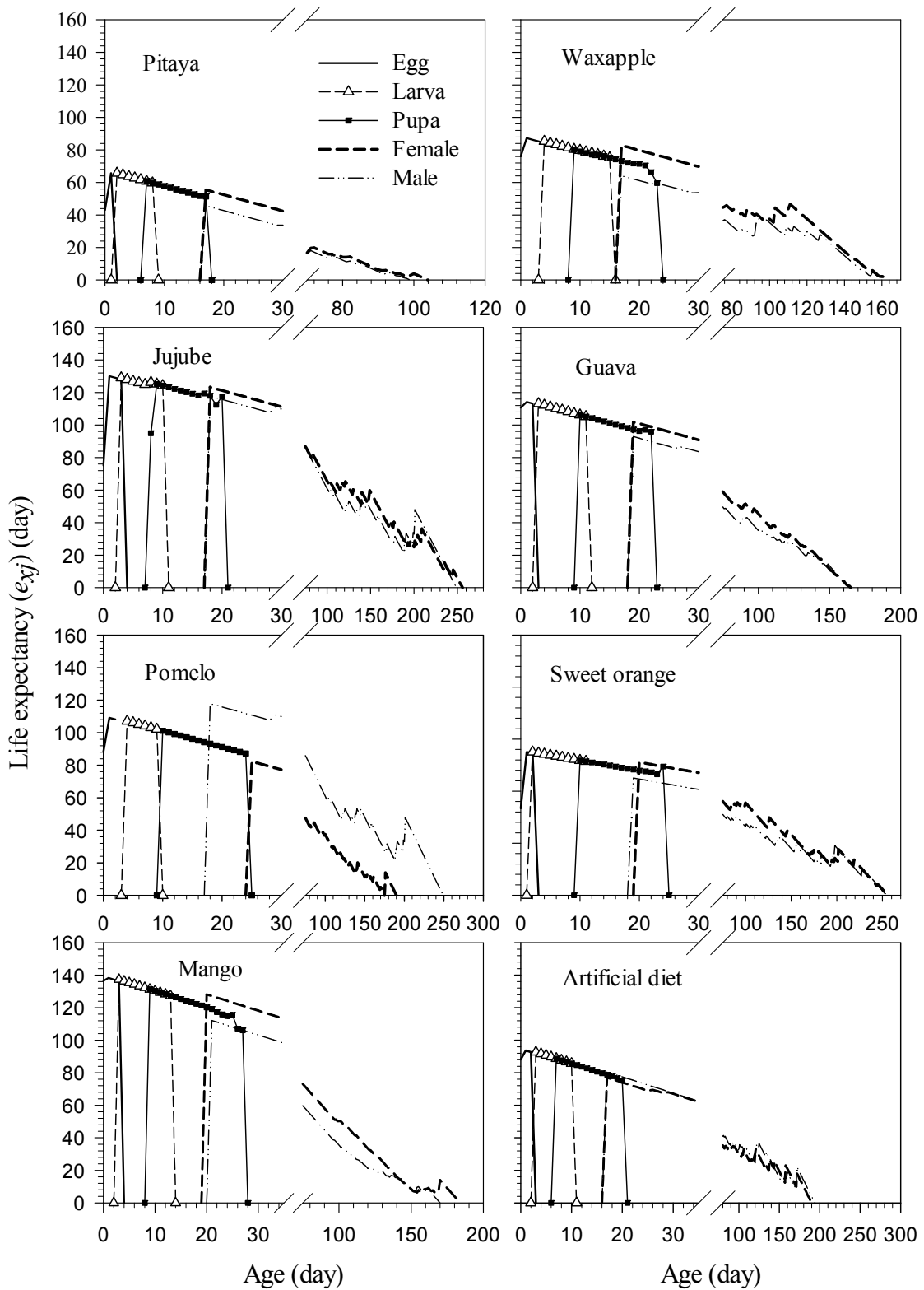


Fig. 3. Age-stage specific life expectancy ( $e_{xj}$ ) of *Bactrocera dorsalis* on different media.

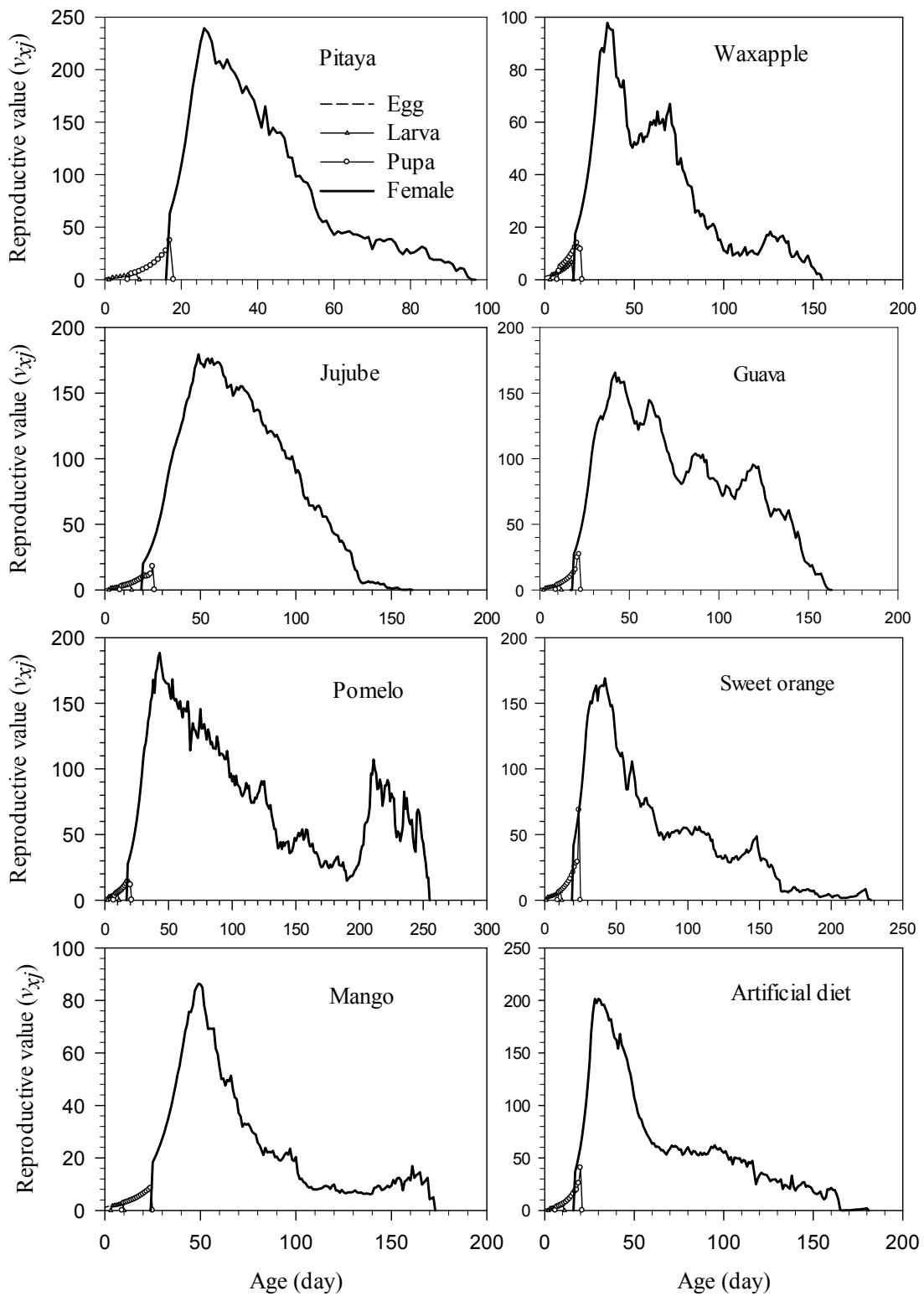


Fig. 4. Age-stage specific reproductive value ( $v_{xj}$ ) of *Bactrocera dorsalis* reared on different media.

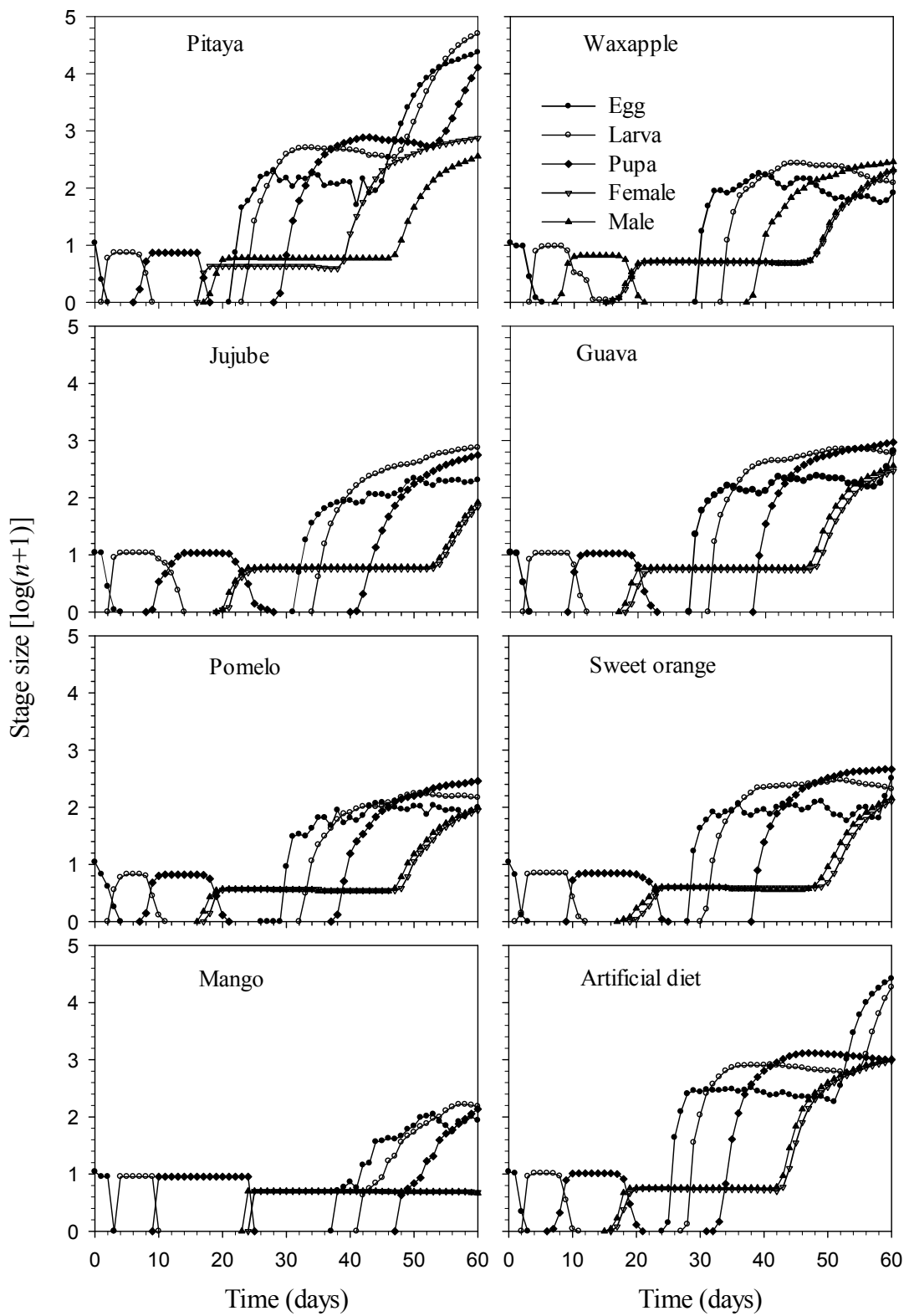


Fig. 5. Projection of population growth *Bactrocera dorsalis* reared on different fruits and an artificial diet with the same initial population of 10 eggs.

## Discussion

Our results showed that *B. dorsalis* could successfully survive and reproduce on seven common fruits (Figs. 1 and 2). Metamorphosis, i.e., stage differentiation, is a unique feature of insects and mites that is also important to pest management because susceptibility varies with stage. However, when the traditional female age-specific life tables (Lewis, 1942; Leslie, 1945; Birch, 1948) were used, it was impossible to show the stage structure, and the stage differentiation would not have been revealed as shown in Fig. 2. Moreover, the inability of traditional female life tables to handle stage differentiation consequently results in the frequent use of “adult age” in the construction of the age-specific fecundity (curve  $m_x$ ). For example, Carey et al. (1988), Lysyk (2001), Kasap & Şekeroğlu (2004), Eilers-Kirk & Fleischer (2006), Haye et al. (2010), Latham & Mills (2010), and Lewontin (1965) noted the importance of the first reproductive age to the intrinsic rate; that is, an earlier reproductive age will generally result in a higher intrinsic rate. In Lewontin (1965), the age was counted from birth. In most entomological literature, scientists used the “adult preoviposition period” (APOP), i.e., the duration from adult emergence to the first reproduction. From the viewpoint of the effect of reproductive age on population increase, a shorter APOP does not always indicate a higher intrinsic rate ( $r$ ) or finite rate ( $\lambda$ ). For example, the APOP of *B. dorsalis* reared on sweet orange was 8.37 d, which was significantly shorter than for those reared on the artificial diet (APOP = 10.98), but the intrinsic rate on sweet orange was  $0.1261 \text{ d}^{-1}$ , which was significantly lower than for those reared on the artificial diet ( $r = 0.1667 \text{ d}^{-1}$ ). On the other hand, the total preoviposition period (TPOP) represents the true duration from birth to the first reproduction. The order of TPOPs of *B. dorsalis* of the eight treatments was pitaya < artificial diet < guava < sweet orange < wax apple < pomelo < jujube < mango, while the order of intrinsic rate was pitaya > guava > artificial diet > sweet orange > wax apple > pomelo > jujube > mango. For *B. dorsalis*, it is safe to conclude that a shorter TPOP may indicate a higher intrinsic rate. In contrast to TPOP, the order of APOP was pitaya < sweet orange < artificial diet < guava < jujube < wax apple < pomelo < mango. A shorter APOP does not always indicate a higher intrinsic rate. Our results showed that TPOP is a more meaningful statistic than APOP. When the reproduction period is short, a shorter TPOP generally indicates a higher value of  $r$  and  $\lambda$  (Gabre et al., 2005). Our results show that the adult preoviposition period (APOP) should be interpreted with caution. However, because the values of  $r$  and  $\lambda$  are not merely dependent on the first reproductive age but also the number of offspring produced at that age, a shorter TPOP does not guarantee a higher growth rate in other insects or under other conditions.

The mean fecundity ( $F$ ) and net reproductive rate ( $R_0$ ) were both calculated from the daily fecundity of females. Chi (1988) proved the relationship between  $F$  and  $R_0$  should be  $R_0 = (N_f / N) \times F$ , where  $N$  is the total number of individuals used at the beginning of life table study (in this study,  $N = 100$  eggs) and  $N_f$  is the number of female adults emerged from  $N$ . All of our results showed a consistent relationship between the net reproductive rate ( $R_0$ ) and the mean fecundity ( $F$ ) as proven by Chi (1988). If the same data were analyzed using a female age-specific life table, such a concrete relationship would not be detected. According to the proof of Chi (1988), and because it is self-evident that  $N_f \leq N$ ,  $R_0 \leq F$  is always true. Unfortunately, in some life tables based on traditional female life tables, the authors reported  $R_0 > F$  (e.g., Liu & Stansly, 1998; Dannon et al., 2010; Milbrath & Biazzo, 2012). Therefore, scientists should pay special attention when applying a traditional female life table to a two-sex population.

A life table is the most comprehensive and important basis of population ecology and pest management. Because insects are ectothermic organisms, their development, survival, and reproduction are significantly affected by abiotic conditions. Moreover, their life tables are affected by host plants. For an effective pest management program, we need to collect life tables of major pests on their main host plants and under different environmental conditions. Population projection is also an important tool for detecting population growth trends, for describing stage structure, and for scheduling the pest management strategies.

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## References

- Agriculture & Food Agency, 2013. Agricultural Statistics Yearbook. Agriculture and Food Agency, Council of Agriculture, Executive Yuan, Taiwan.
- Bateman, M.A. 1972. The ecology of fruit flies. *Annual Review of Entomology*, 17: 493-518.
- Birch, L.C. 1948. The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology*, 17: 15-26.
- CABI & EPPO, 1997. Quarantine Pests for Europe. CAB International and European and Mediterranean Plant Protection Organization, New York, USA.
- Carey, J.R. 2001. Insect biodemography. *Annual Review of Entomology*, 46: 79-110.
- Carey, J.R., P.J. Yang, & D. Foote, 1988. Demographic analysis of insect reproductive levels, patterns and heterogeneity: case study of laboratory strains of three Hawaiian tephritids. *Entomologia Experimentalis et Applicata*, 46: 85-91.
- Chi, H. 1988. Life-table analysis incorporating both sexes and variable development rates among individuals. *Environmental Entomology*, 17: 26-34.
- Chi, H. 1990. Timing of control based on the stage structure of pest populations: a simulation approach. *Journal of Economic Entomology*, 83: 1143-1150.
- Chi, H. 2013. TWSEX-MS Chart: a computer program for the age-stage, two-sex life table analysis. <http://140.120.197.173/Ecology/Download/TwoSEX-MSChart.zip>.
- Chi, H. 2014. TIMING-MS Chart: a computer program for the population projection based on age-stage, two-sex life table. <http://140.120.197.173/Ecology/Download/Timing-MSChart.zip>.
- Chi, H. & H. Liu, 1985. Two new methods for the study of insect population ecology. *Bulletin of the Institute of Zoology, Academia Sinica*, 24: 225-240.
- Chi, H. & H.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. *Environmental Entomology*, 35: 10-21.
- Dannon, E.A., M.A. Tamò, A. van Huis & M. Dicke, 2010. Functional response and life history parameters of *Apanteles taragamae*, a larval parasitoid of *Maruca vitrata*. *BioControl*, 55: 363-378.
- Efron, B. & R.J. Tibshirani, 1993. *An Introduction to the Bootstrap*. Chapman & Hall, New York, NY.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford, United Kingdom.
- Ellers-Kirk, C. & S.J. Fleischer, 2006. Development and life table of *Acalymma vittatum* (Coleoptera: Chrysomelidae), a vector of *Erwinia tracheiphila* in cucurbits. *Environmental Entomology*, 35: 875-880.
- Foote, D. & J.R. Carey, 1987. Comparative demography of laboratory and a wild strain of the oriental fruit fly, *Dacus dorsalis*. *Entomologia Experimentalis et Applicata*, 44: 263-268.
- Gabre, R.M., F.K. Adham & H. Chi, 2005. Life table of *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae). *Acta Oecologia*, 27: 179-183.
- Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. *The American Naturalist*, 119: 803-823.
- Guo, J.Y., L. Cong, Z.S. Zhou, & F.H. Wan, 2012. Multi-generation life tables of *Bemisia tabaci* (Gennadius) biotype B (Hemiptera: Aleyrodidae) under high-temperature stress. *Environmental Entomology*, 41: 1672-1679.
- Haye, T., P.G. Mason, L.M. Dossall & U. Kuhlmann, 2010. Mortality factors affecting the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham), in its area of origin: A life table analysis. *Biological Control*, 54: 331-341.
- Huang, Y.B. & 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 Science*, 19: 803-823.

- Huang, Y.B. & 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). *Journal of Agriculture and Forestry*, 61: 37-45.
- Huang, Y.B. & H. Chi, 2013. Life tables of *Bactrocera cucurbitae* (Diptera: Tephritidae): with an invalidation of the jackknife technique. *Journal of Applied Entomology*, 137: 327-339.
- Kasap, İ. & E. Şekeroğlu, 2004. Life history of *Euseius scutalis* feeding on citrus red mite *Panonychus citri* at various temperatures. *BioControl*, 49: 645-654.
- Latham, D.R. & N.J. Mills, 2010. Life history characteristics of *Aphidius transcaspicus*, a parasitoid of mealy aphids (Hyalopterus species). *Biological Control*, 54: 147-152.
- Legaspi, J.C., C. Mannion, D. Amalin, & B.C. Legaspi Jr, 2011. Life table analysis and development of *Singhiella simplex* (Hemiptera: Aleyrodidae) under different constant temperatures. *Annals of the Entomological Society of America*, 104: 451-458.
- Leslie, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika*, 33: 183-212.
- Lewis, E.G. 1942. On the generation and growth of a population. *Sankhya*, 6: 93-96.
- Lewontin, R.C. 1965. "Selection for Colonizing Ability, 77-94". In: *The Genetic of Colonizing Species* (Eds, H.G. Baker & G.L. Stebbins.). Academic Press, San Diego, CA.
- Liu, T.X. & P.A. Stansly, 1998. Life history of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on *Hibiscus rosa-sinensis* (Malvaceae). *The Florida Entomologist*, 81: 437-445.
- Lysyk, T.J. 2001. Relationships between temperature and life history parameters of *Muscidifurax raptorellus* (Hymenoptera: Pteromalidae). *Environmental Entomology*, 30: 982-992.
- Milbrath, L.R. & J. Biazzo, 2012. Development and reproduction of the foxglove aphid (Hemiptera: Aphididae) on invasive swallow-worts (*Vincetoxicum* spp.). *Environmental Entomology*, 41: 665-668.
- Muştu, M. & N. Kılınçer, 2013. Life table and some feeding features of *Nephus kreissli* fed on *Planococcus ficus*. *Phytoparasitica*, 41:203-211.
- Núñez-Campero, S.R., M. Aluja, J. Rull, & S.M. Ovruski, 2014. Comparative demography of three neotropical larval-prepupal parasitoid species associated with *Anastrepha fraterculus* (Diptera: Tephritidae). *Biological Control*, 69: 8-17.
- Polat Akköprü, E., R. Atlıhan, 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. *Journal of Economic Entomology* (in press).
- Tanaka, N., L.F. Steiner, K. Ohinata & R. Okamoto, 1969. Low-cost larval rearing medium for mass production of oriental and Mediterranean fruit flies. *Journal of Economic Entomology*, 62: 967-968.
- Tuan, S.J., C.C. Lee & H. Chi, 2014. 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 Management Science*, 70: 805-813.
- Vargas, R.I. & J.R. Carey, 1990. Comparative survival and demographic statistics for wild oriental fruit fly, Mediterranean fruit fly, and melon fly (Diptera: Tephritidae) on papaya. *Journal of Economic Entomology*, 83: 1344-1349.
- Vargas, R.I., J.D. Stark & T. Nishida, 1990. Population dynamics, habitat preference, and seasonal distribution patterns of oriental fruit fly and melon fly (Diptera: Tephritidae) in an agricultural area. *Environmental Entomology*, 19: 1820-1828.
- Vargas, R.I., W.A. Walsh, D. Kanehisa, E.B. Jang & J.W. Armstrong, 1997. Demography of four Hawaiian fruit flies (Diptera: Tephritidae) reared at five constant temperatures. *Annals of the Entomological Society of America*, 90:162-168.
- Vargas, R.I., W.A. Walsh, D. Kanehisa, J.D. Stark & T. Nishida, 2000. Comparative demography of three Hawaiian fruit flies (Diptera: Tephritidae) at alternating temperatures. *Annals of the Entomological Society of America*, 93: 75-81.