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Using two-sex life tables to determine fitness parameters of four *Bactrocera* species (Diptera: Tephritidae) reared on a semi-artificial diet

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Abstract

Fruit flies in the genus *Bactrocera* are global, economically important pests of agricultural food crops. However, basic life history information about these pests, which is vital for designing more effective control methods, is currently lacking. Artificial diets can be used as a suitable replacement for natural host plants for rearing fruit flies under laboratory conditions, and this study reports on the two-sex life-table parameters of four *Bactrocera* species (*Bactrocera correcta*, *Bactrocera dorsalis*, *Bactrocera cucurbitae*, and *Bactrocera tau*) reared on a semi-artificial diet comprising corn flour, banana, sodium benzoate, yeast, sucrose, winding paper, hydrochloric acid and water. The results indicated that the larval development period of *B. correcta* (6.81 ± 0.65 days) was significantly longer than those of the other species. The fecundity of *B. dorsalis* (593.60 eggs female^{-1}) was highest among the four species. There were no differences in intrinsic rate of increase (r) and finite rate of increase (λ) among the four species. The gross reproductive rate (*GRR*) and net reproductive rate (R_0) of *B. dorsalis* were higher than those of the other species, and the mean generation time (T) of *B. cucurbitae* (42.08 ± 1.21 h) was longer than that of the other species. We conclude that the semi-artificial diet was most suitable for rearing *B. dorsalis*, due to its shorter development time and higher fecundity. These results will be useful for future studies of fruit fly management.

Keywords: *Bactrocera*, fruit flies, fitness, semi-artificial diet, Tephritidae, two-sex life table

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Introduction

Globally, fruit flies (Diptera: Tephritidae) are significant pests of agricultural crops in Asia since the beginning of the last century. Species in the genus *Bactrocera* have been reported to potentially infest more than 173 kinds of fruits and vegetables (Gupta & Verma, 1978; White & Elson-Harris, 1992; Allwood *et al.*, 1999; Drew & Raghu, 2002; Dhillon *et al.*, 2005; Ekesi *et al.*, 2016), where internal feeding by larvae causes premature abscission of fruit (Shinwari *et al.*, 2015).

Within the *Bactrocera* genus, *Bactrocera correcta* (Bezzi), *Bactrocera dorsalis* (Hendel), *Bactrocera cucurbitae* (Coquillet) *and Bactrocera tau* (Walker) have been considered economically important and widely distributed pests of agricultural crops including fruits, vegetables and nuts all over the world (Drew, 2004; Clarke *et al.*, 2005). The *B. correcta* (the guava fruit fly) has been listed as a quarantine pest in most Asian countries (Tan *et al.*, 2011; Jiang *et al.*, 2013), and studies have reported that it could cause significant damage to commercial

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fruit crops in Thailand and Vietnam (Drew & Raghu, 2002; Liu *et al.*, 2013). The *B. dorsalis* is known to utilize more than 250 host plants, and as a result of this wide host plant range, its infestation tends not to be recorded above the economic injury level of 7.5% at the time of harvest in high-value crops such as carambola (star fruit) (Jiang *et al.*, 2017). In contrast, high levels of infestation by other *Bactrocera* species have been reported: for example, 41–89% infestation rates by *B. cucurbitae* in bitter gourd (Lall & Sinha, 1959; Kushwaha *et al.*, 1973). In Asia, approximately 15–40% losses in fruit are caused by *B. tau* infestation (Hasyim *et al.*, 2016). And the losses level varies from 30 to 100% (Gupta & Verma, 1978; Dhillon *et al.*, 2005), which depends on the infested vegetable species and seasons.

Integrated pest management (IPM) techniques are very important for the management of *Bactrocera* species in farms and orchards (Kogan & Bajwa, 1999). In IPM programs, it is necessary to understand the basic and detailed information of pests, such as survival, development and reproduction rates, and this information can be derived through life table modeling (Yang *et al.*, 1994; Vargas *et al.*, 2000). However, traditional life table models only provide information for female age-specific populations (Leslie, 1945; Birch, 1948; Lewis, 1977), whereas models for both males and females are needed to understand ecology, population dynamics, and survival (Huang & Chi, 2012, 2013).

In order to compile species life tables, insects usual are reared on artificial diets under laboratory conditions, since it is difficult to use the natural hosts during the whole year (Chang *et al.*, 2004). An artificial diet is defined as 'an unfamiliar food which has been formulated, synthesized, processed, and/or concocted by humans, on which an insect in captivity can develop through all or part of its life cycle' (Singh, 1977). While different artificial diets have been successfully prepared for the rearing of economically important pests, most of these species were lepidopterans (Castañé & Zapata, 2005). The preparation of a larval diet for the mass rearing of *Bactrocera* fruit flies has long been considered an important area of research and there have been some developments: *Bactrocera* survival, growth and developmental rates were improved using dry plant materials, sugars and yeasts in an artificial diet (Vargas & Carey, 1989; Rajaganapathi & Kathiresan, 2002; Liu *et al.*, 2015; Rabab *et al.*, 2016), whereas banana was found to be an important fruit for the preparation of semi-artificial diet (Rabab *et al.*, 2016). Although a banana-based, semi-artificial diet for rearing larval *B. dorsalis* to study the olfactory behavior in male adults (Liu *et al.*, 2015), no studies have been done on the fitness of male and female fruit flies of *Bactrocera* complex species on the semi-artificial diet.

In order to improve widely the methods for mass rearing of *Bactrocera* flies to gain an better understanding of their life history, the objective of this study was to assess male and female fitness of four species of economically important *Bactrocera* flies including *B. correcta*, *B. dorsalis*, *B. cucurbitae*, and *B. tau*, on a banana-based, semi-artificial diet, under laboratory conditions to create two-sex life tables.

Materials and methods

Insects

Cultures of *B. correcta*, *B. dorsalis*, *B. cucurbitae*, and *B. tau* were established in 2016 at the College of Agriculture, South China Agricultural University, Guangzhou, China. Prior to the experiment, the flies were reared for least two generations to allow for acclimatization to the semi-artificial diet and laboratory conditions. Adult flies were reared in cages (30 × 30 × 30 cm^3) by providing water-soaked cotton wool in a box (12 × 6.8 × 7 cm^3) and powdered yeast and sugar (2:1) in petri-dish (6 × 1.5 cm^2). Fruit fly rearing and experimental study were carried out in a controlled room set at 25 ± 2°C, 60 ± 5% relative humidity, and a photoperiod of L:D 14:10 h. The temperature was controlled by the air-conditioner (Gree Electric Appliances, Inc. of Zhuhai, Zhuhai, China) and the humidity was maintained by humidifier.

Fig. 1. Plastic bottles (a) perforated and filled with banana and pumpkin into which eggs were laid; and (b) to record fecundity of adult female fruit flies.

Diet preparation

The semi-artificial diet was prepared according to the method of Liu *et al.* (2015) and comprised 150 g corn flour, 30 g yeast, 30 g sucrose and 30 g fiber as well as 150 g banana that were measured on an electronic weighing balance (AB204-N, Mettler Toledo, Boston, USA) and then mixed together in an electronic blender (OPY-908, Zhongshan Opaye Industry Co., Ltd., Zhongshan, China). To this dry mixture, 0.6 g sodium benzoate, as an anti-microbial, and 1.2 ml hydrochloric acid and 300 ml water were added and mixed to make a semi solid diet (Liu *et al.*, 2015).

Life table parameters

To determine life table parameters for male and female flies, eggs which had been laid within 24 h were selected. Eggs were collected from banana and pumpkin that had been placed in plastic bottles (11 × 4 cm^2) perforated with

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Table 1. Fitness parameters of *B. correcta*, *B. dorsalis*, *B. cucurbitae* and *B. tau*.

Parameters	*B. correcta*	*B. dorsalis*	*B. cucurbitae*	*B. tau*
Egg duration	1.71 ± 0.05b	1.67 ± 0.06b	2.21 ± 0.08a	1.69 ± 0.09b
Total larval duration	6.81 ± 0.65a	5.99 ± 0.44b	6.30 ± 0.20b	5.44 ± 0.34c
1st instar	1.22 ± 0.05b	1.44 ± 0.04a	1.49 ± 0.05a	1.06 ± 0.02c
2nd instar	1.61 ± 0.04b	1.70 ± 0.05ab	1.86 ± 0.09a	1.73 ± 0.09b
3rd instar	3.98 ± 0.06a	2.85 ± 0.10b	2.95 ± 0.08b	2.83 ± 0.13b
Pupal duration	7.39 ± 0.25ab	6.77 ± 0.17b	7.81 ± 0.20a	7.92 ± 0.20a
Male longevity	119.62 ± 3.96c	141.43 ± 1.27b	151.47 ± 2.70a	138.05 ± 3.57b
Female longevity	139.00 ± 3.16d	150.42 ± 3.26c	162.46 ± 3.12a	153.25 ± 2.40b
APOP/APRP	12.45 ± 0.26c	16.83 ± 0.21a	16.23 ± 0.27a	15.70 ± 0.25b
TPOP/TPRP	28.36 ± 0.58c	32.08 ± 1.44a	33.77 ± 1.01a	30.58 ± 0.99b
Oviposition	18.55 ± 0.33b	21.75 ± 0.63a	21.15 ± 0.22a	21.00 ± 0.28a
Fecundity	393.60 ± 9.96d	593.60 ± 5.96a	463.70 ± 6.18c	511.30 ± 3.44b

APOP, adult pre-oviposition period; APRP, adult pre-reproduction period; TPOP, total pre-oviposition period of female counted from emergence, TPRP, total pre-reproduction period of female counted from emergence.
With the exception of fecundity (eggs female^{-1}), units are days.
Means rows followed by the same letter are not significantly different ($P > 0.05$) using bootstrap test.

1 mm diameter holes (fig. 1a) that had, in turn, been placed in the above mentioned rearing cages. The bottle's surface was considered as an oviposition substrate. Eggs were collected by soft hair brush and shifted into jar (12 × 6 × 6 cm^3) that contained semi-artificial diet. The jars were covered with muslin cloth. Five eggs of each species were placed into a jar. This experiment was replicated ten times. The developmental condition of each species, from egg to adult formation, was recorded daily. Puparia were removed to a separate plastic box (23.5 × 15.8 cm^2) containing a 3-cm layer of sand, before adult emergence. After emergence, adults were sexed; one pair of flies (one female and one male) per species was introduced into a plastic jar (18 × 16 × 16 cm^3) as a replication. Ten replications per species were conducted for this experiment. A small plastic bottle (4 × 1 cm^2; perforated with 1 mm diameter holes, and contained banana and pumpkin) was kept in each plastic jar for fecundity recording (fig. 1b).

Biological/Fitness parameters were recorded daily, comprising duration (days) of adult developmental stages; adult pre-oviposition period (APOP) or adult pre-reproduction period (APRP) of adult females; total pre-oviposition period (TPOP) or total pre-reproduction period (TPRP) of female counted from birth; oviposition duration (days); and, fecundity. Body weights of immature and mature stages of each fly were measured on an electronic weighing balance (Chi & Su, 2006; Singh *et al.*, 2010), while body lengths and widths of immature and mature stages were measured using a Keyence VHX-5000 digital microscope, according to the method by Pozuelo *et al.* (2015).

Statistical analysis

The biological/fitness parameters included development duration of both immature and mature stage, APOP, TPOP, oviposition and fecundity were calculated in the computer program TWO-SEX-MS Chart (Chi & Team, 2017) in VISUAL BASIC (version 6, service pack 6) for the Windows system (http://140.120.197.173/Ecology and http://nhsbig.inhs.uiuc.edu/wes/chi.html). The population life table parameters (intrinsic rate of increase (r), finite rate of increase (λ), gross reproductive rate (GRR), net reproductive rate (R_0), doubling time (DT) and the mean generation time (T) were estimated according to the method described by Chi & Su (2006).

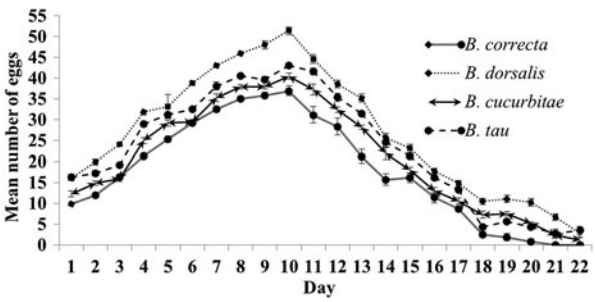

Fig. 2. Daily reproduction dynamics of adult females of *B. correcta*, *B. dorsalis*, *B. cucurbitae*, and *B. tau* on artificial diet.

In this study, the intrinsic rate of increase is estimated using the iterative bisection method from the Euler-Lotka formula with age indexed from 0 (Goodman, 1982), as shown in Equation 1.

$$\sum_{n=0}^{\infty} \binom{n}{k} e^{-r(x+)} lxMx = 1 \quad (1)$$

The mean generation time is defined as the length of time that a population needs to increase to R_0-fold of its size (i.e. $e^{rT} = R_0$ or $\lambda^T = R_0$) (Chi & Su, 2006). The life table parameters of each species were repeated three times to confirm the data. The differences between means were compared using least significant difference (LSD) with the statistics program SAS (SAS Institute, 2009) with PROCGLM and bootstrap tests ($P > 0.05$).

Results

Fly development

Significant differences in development times, from egg to pupation, among *B. correcta*, *B. dorsalis*, *B. cucurbitae*, and *B. tau* were recorded and analyzed (table 1). The incubation period (time between laying and hatching) for *B. cucurbitae* was significantly longer than for *B. dorsalis*, *B. correcta*, and *B. tau* ($F_{3,76} = 2.9$, $P < 0.05$). The total larval period of *B. correcta* was significantly longer than for *B. dorsalis*, *B. cucurbitae*, and *B. tau* ($F_{3,76} = 20.1$, $P < 0.05$). Comparison of adult male and female longevity showed females lived longer than males (table 1).

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Table 2. Life table parameters of *B. correcta*, *B. dorsalis*, *B. cucurbitae* and *B. tau*.

Parameters	*B. correcta*	*B. dorsalis*	*B. cucurbitae*	*B. tau*
R	0.118 ± 0.001a	0.119 ± 0.003a	0.109 ± 0.003a	0.118 ± 0.004a
Λ	1.125 ± 0.011a	1.126 ± 0.017a	1.115 ± 0.011a	1.127 ± 0.013a
GRR	89.79 ± 3.21c	137.42 ± 6.79a	114.65 ± 5.31b	116.84 ± 4.98b
R_0	71.83 ± 3.61c	119.1 ± 4.31a	99.36 ± 3.11b	101.26 ± 4.71b
T	36.23 ± 0.21d	40.31 ± 1.41b	42.08 ± 1.21a	38.69 ± 1.21c
DT	5.87 ± 0.23a	5.84 ± 0.34a	6.34 ± 0.34a	5.80 ± 0.54a
Birth rate (at SASD)	0.13 ± 0.001a	0.13 ± 0.002a	0.12 ± 0.005a	0.13 ± 0.004a
Survival rate (at SASD)	0.991 ± 0.02a	0.995 ± 0.04a	0.995 ± 0.003a	0.995 ± 0.004a
Death rate (at SASD)	8.93 ± 1.21a	5.00 ± 1.14b	4.90 ± 1.32b	5.05 ± 1.32b

r, intrinsic rate of increase (day^{-1}); λ, finite rate of increase (day^{-1}); *GRR*, gross reproductive rate (offspring individual^{-1}); R_0, net reproductive rate (offspring individual^{-1}); *T*, mean generation time (days); and, *DT*, Doubling time.
Means in rows followed by the same letter are not significantly different ($P > 0.05$) using bootstrap test.

Table 3. The body weight of development stages *B. correcta*, *B. dorsalis*, *B. cucurbitae and B. tau*.

	Body weight (g)			
Development stage	*B. correcta*	*B. dorsalis*	*B. cucurbitae*	*B. tau*
1st instar	0.0116 ± 0.0003d	0.0180 ± 0.0005a	0.0172 ± 0.0006b	0.0134 ± 0.0005c
2nd instar	0.0219 ± 0.0004d	0.0283 ± 0.0003a	0.0264 ± 0.0004b	0.0253 ± 0.0003c
3rd instar	0.0318 ± 0.0004d	0.0374 ± 0.0004a	0.363 ± 0.0002b	0.0339 ± 0.0002c
Pupa	0.0420 ± 0.0004d	0.0475 ± 0.0007a	0.0463 ± 0.0005b	0.0450 ± 0.0002c
Male	0.0529 ± 0.0010c	0.0631 ± 0.0005a	0.0607 ± 0.0006b	0.0609 ± 0.0050b
Female	0.0586 ± 0.0030d	0.0695 ± 0.0020a	0.0678 ± 0.0020b	0.0648 ± 0.0010c

Means in rows followed by the same letter are not significantly different ($P > 0.05$) using LSD test.

The life spans of *B. cucurbitae* males and females were significantly greater than those of the other species (males: $F_{3,76} = 8.28$, $P < 0.001$; females: $F_{3,76} = 47.0$, $P < 0.001$; table 1).

There was no significant difference in the APOP of female adults for *B. dorsalis* and *B. cucurbitae*. However, the durations of APRP for these species were significantly longer than those for *B. correcta* and *B. tau* ($F_{3,36} = 39.3$, $P < 0.001$). TPOP was remarkably longer in female *B. dorsalis* than in the other three species ($F_{3,36} = 12.3$, $P < 0.001$; table 1).

Mean daily egg production rate curves for *B. correcta*, *B. dorsalis*, *B. cucurbitae*, and *B. tau* were shown in fig. 2. Mean egg production rate curve of female *B. dorsalis* was the highest one among the four tested species (fig. 2). Fecundity in *B. dorsalis* was significantly higher than those in the other three species ($F_{3,36} = 139$, $P < 0.001$; table 1).

Population life table parameters

There was no significant difference in the intrinsic rate of increase and finite rate of increase per day among the four species of *Bactrocera*. The *GRR* and R_0 for *B. dorsalis* (137.4 and 119.1 offspring individual^{-1}, respectively) were higher than *B. correcta*, *B. cucurbitae* and *B. tau* (table 2). Mean generation time for *B. cucurbitae* was longer than those for *B. correcta*, *B. dorsalis* and *B. tau*; however, there was no difference in the *DT* among four species (table 2).

Body weight

There were significant differences in body weight of immature and mature stages among four species, where *B. dorsalis* gained the greatest body weight. The body weights of larval *B. dorsalis* were greater than those of other three species (the first instar larvae: $F_{3,36} = 433$, $P < 0.001$; the second instar larvae: $F_{3,36} = 526$, $P < 0.001$; and the third instar larvae: $F_{3,36} = 534$, $P < 0.001$, respectively). Similarly, the pupal body weight of *B. dorsalis* was significantly greater than those of the other three species ($F_{3,36} = 245$, $P < 0.001$). Adult male ($F_{3,36} = 510$, $P < 0.001$) and female ($F_{3,36} = 532$, $P < 0.001$) flies of *B. dorsalis* gained the highest body weight among the tested four species (table 3).

Body size

The immature and mature stages of *B. correcta*, *B. dorsalis*, *B. cucurbitae* and *B. tau* were shown in fig. 3. Mean body length and width of immature and mature stages of *B. dorsalis*, *B. correcta*, *B. cucurbitae* and *B. tau* were significantly different from each other (table 4), the mean egg length ($F_{3,36} = 1.01$, $P < 0.001$) and width ($F_{3,36} = 1.01$, $P < 0.001$) of *B. tau* were greater than those of other *Bactrocera* flies. A similar trend was observed for other immature stages (first, second, third instar and pupa) of *B. tau* (table 4). Mean body lengths of male ($F_{3,36} = 309$, $P < 0.001$) and female ($F_{3,36} = 416$, $P < 0.001$) adult *B. tau* were significantly longer than those of other three species. Mean wing length of female *B. cucurbitae* was significantly longer than those of other three species ($F_{3,36} = 23.74$, $P < 0.001$). Mean thorax ($F_{3,36} = 247$, $P < 0.001$) and abdomen ($F_{3,36} = 248$, $P < 0.001$) widths of male adult of *B. dorsalis* were significantly longer than those of other three species. Similarly, the same trend was recorded for the thorax ($F_{3,36} = 292$, $P < 0.001$) and abdomen ($F_{3,36} = 49.8$, $P < 0.001$) width of female adults of *B. dorsalis* (table 4).

Discussion

Several studies have described the biology of *Bactrocera* species on different natural host plants and artificial diet

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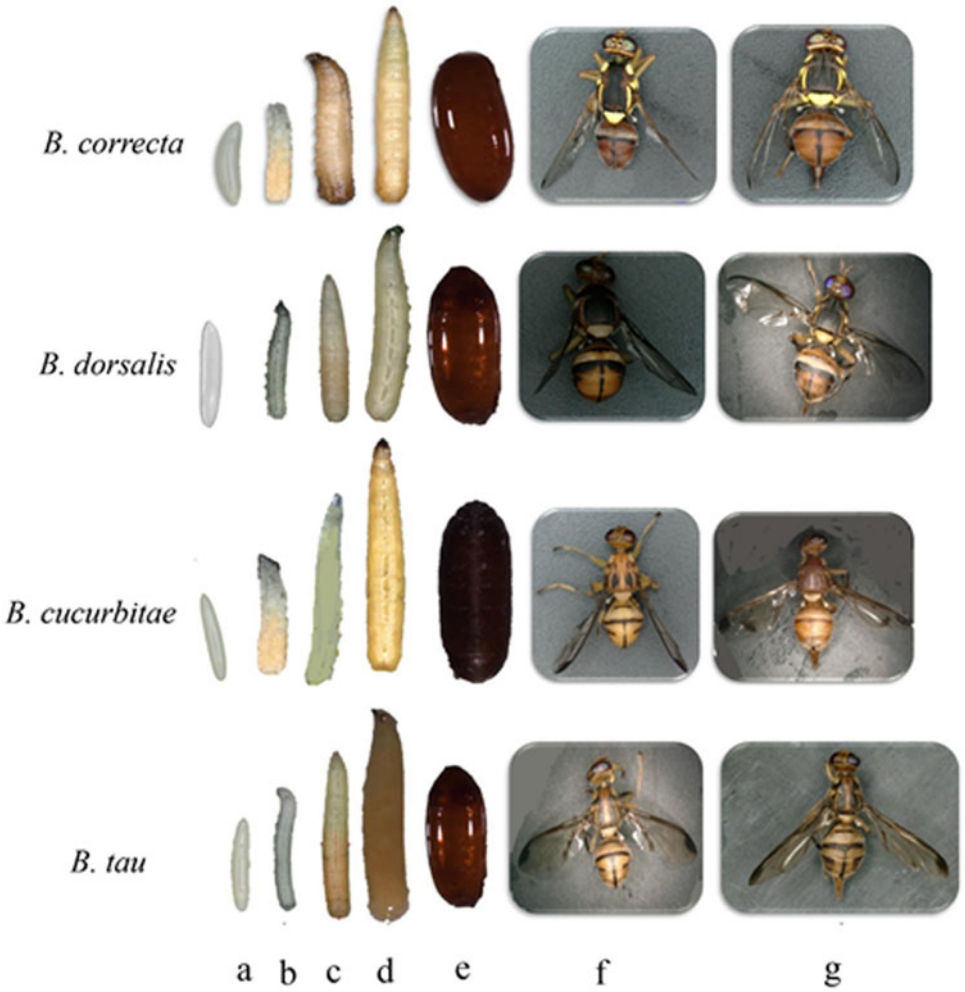

Fig. 3. Different stages of *Bactrocera* species fed on the semi-artificial diet. (a) egg; (b) first instar; (c) second instar; (d) third instar; (e) pupa; (f) male adult; and, (g) female adult.

(Ekesi *et al.*, 2007; Vayssières *et al.*, 2008; Waseem *et al.*, 2012; Mir *et al.*, 2014), with a few studies having focused on the two-sex life table traits of *B. cucurbitae* on cucumber as a natural host plant (Huang & Chi, 2012; 2013). Our study, first time described the two-sex life table parameters of four species in the genus *Bactrocera* e.g., *B. correcta*, *B. dorsalis*, *B. cucurbitae* and *B. tau* fed on semi-artificial diet.

The development of immature insect pests is known to fluctuate with various abiotic and biotic factors, including light, temperature and humidity, and food resource, predation and competition, respectively (Shen *et al.*, 2014; Chen *et al.*, 2017). When controlling for other factors, optimum food resource for development of insect pests is typified by shortest life cycles and highest levels of fecundity (Awmack & Leather, 2002). In our study, we found that *B. dorsalis* responded better to the semi-artificial diet than other three species, since it had the shortest life cycle and highest fecundity (table 1).

Semi-artificial diets including inert bulking agents, such as tissue papers and cotton wool soaked with fluid have been used successfully for small scale rearing of *Ceratitis capitata* (Wiedemann) and *Rhagoletis cerasi* L. (Katsoyannos *et al.*, 1977; Rajaganapathi & Kathiresan, 2002). The biology of *B. olae* has been successfully studied on two types of artificial diets (cotton toweling and liquid diet) (Mittler & Tsitsipis, 1973), while *B. cucurbitae* and *B. tryoni* have been reared on a liquid diet, with wheat-based bulking agent and oil, but there were high costs associated with diet management (disposal and tray cleaning), storage, space, labor, and sanitation (Changmu & Hongmu, 2006; Dominiak *et al.*, 2010). Our study successfully described the fitness of four *Bactrocera* species reared on a semi-artificial diet that was prepared with low associated costs.

Pupal development period and weight are important key factors for the survival of insect pests, especially in fruit flies, where the high pupal body weight is positively related to high fecundity. We found the highest pupal body weight and fecundity in *B. dorsalis* fed on the semi-artificial diet. The development time of the immature stages appears to vary with food resource, because the pupal period of *B. cucurbitae* was completed in 8–9 days on a cucumber diet (Waseem *et al.*, 2012), while in our study completion took 6–7 days.

The pre-oviposition period of *B. cucurbitae* has been reported as 10–15 days by Mir *et al.* (2014). In our study, pre-oviposition of *B. cucurbitae* was 16.23 days. Huang & Chi

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Table 4. Mean body length and width of *B. correcta, B. dorsalis, B. cucurbitae and B. tau*.

Development stages	Parameters (mm)	*B. correcta*	*B. dorsalis*	*B. cucurbitae*	*B. tau*
Egg	L	1.08 ± 0.01d	1.15 ± 0.02c	1.26 ± 0.01b	1.41 ± 0.01a
	W	0.27 ± 0.00d	0.29 ± 0.01c	0.32 ± 0.00b	0.35 ± 0.00a
1st instar	L	2.57 ± 0.11d	3.65 ± 0.01c	3.69 ± 0.01b	3.73 ± 0.01a
	W	0.84 ± 0.01d	1.18 ± 0.03c	1.03 ± 0.02b	1.13 ± 0.01a
2nd instar	L	4.74 ± 0.01d	5.65 ± 0.02c	5.85 ± 0.01b	6.03 ± 0.01a
	W	1.13 ± 0.01d	1.42 ± 0.01c	1.46 ± 0.01b	1.48 ± 0.01a
3rd instar	L	8.34 ± 0.02d	8.85 ± 0.02c	9.03 ± 0.00b	9.09 ± 0.01a
	W	1.48 ± 0.01d	1.83 ± 0.01c	1.85 ± 0.01b	1.89 ± 0.01a
Pupa	L	4.94 ± 0.01d	5.47 ± 0.05c	5.83 ± 0.00b	5.89 ± 0.02a
	W	2.27 ± 0.02c	2.39 ± 5.83b	2.43 ± 0.00a	2.39 ± 0.01b
Male	L	5.65 ± 0.01d	7.76 ± 0.01c	8.03 ± 0.01b	8.06 ± 0.04a
	Thorax W	2.03 ± 0.01c	2.88 ± 0.00a	2.19 ± 0.00bc	2.39 ± 0.10b
	Abdomen W	2.28 ± 0.00d	2.42 ± 0.01a	2.39 ± 0.01b	2.35 ± 0.01c
	Wing L	4.59 ± 0.01d	6.03 ± 0.01c	6.18 ± 0.02a	6.13 ± 0.00b
Female	Length	6.67 ± 0.35b	8.77 ± 0.34ab	8.89 ± 0.23ab	9.01 ± 0.23a
	Thorax W	2.18 ± 0.02c	2.37 ± 0.01a	2.38 ± 0.02a	2.34 ± 0.01b
	Abdomen W	2.40 ± 0.03d	2.52 ± 0.03a	2.49 ± 0.01b	2.43 ± 0.01c
	Wing L	5.62 ± 0.00d	6.12 ± 0.04c	6.21 ± 0.23a	6.18 ± 0.01b

L, length; W, width.
Means in rows followed by the same letter are not significantly different ($P > 0.05$) using LSD test.

(2012) reported that the total pre-adult development time of *B. cucurbitae* was 15.1 days at 25°C on the natural host (cucumber) and Vayssières *et al.* (2008) reported 17.2 and 13.2 days, at 25 and 30°C respectively. In our study, we found total pre-adult development times for this species reared at 25°C was 16.23 days. In comparison with natural host plant as diets, this quicker development time might be due to the artificial food and rearing conditions. In IPM, application of management tactics for *Bactrocera* species would be more useful at pupal and pre-oviposition period rather than other stages.

Fecundity rates are known to vary among species; according to Vargas *et al.* (1997), fecundity of *B. dorsalis* was greater than that of *B. cucurbitae* when reared on natural host plant material. In this study, we also found that fecundity of *B. dorsalis* was greater than that of *B. cucurbitae*. Furthermore, temperature-related differences in fecundity have been found in fruit flies. For example, Changmu & Hongmu (2006) found the mean fecundity of *B .cucurbitae* reared on a cucumber diet at 30°C was 896 eggs female^{-1}, while Mir *et al.* (2014) found the fecundity range was 58–92 eggs at 23.97 ± 0.66°C and our study showed a rate of 463.7 eggs female^{-1} at a temperature of 25°C. Differences in longevity between males and females, which we found in our study, have also been reported elsewhere, where females tend to live longer than males (Mir *et al*., 2014).

Concerning biology and bionomics of *B. tau*, the detailed parameters of larval instars were not described (Singh *et al.*, 2010). In our study, the body length and width of these flies were higher than those reported by Singh *et al.* (2010). It may reflect a difference in rearing medium and food source. The intrinsic rate of increase (r) is an important population parameter in insect development and survival, because it explains the age, sex ratio, survivorship, and fecundity of insect population (Varley & Gradwell, 1970). If r is greater than 0, then it might be the most appropriate population index to describe the adaptation of an insect to a food resource (Razmjou & Golizadeh, 2010; Chen *et al*., 2017). Indeed, we found that the r values for the four *Bactrocera* species were greater than zero, indicating suitability of the semi-artificial diet. The net reproductive rate is an indicator of rate of population increase, where the highest rate of population increase is dependent on the fecundity, development and survival of insect pests (Sayyed *et al*., 2008; Huang & Chi, 2012). According to life tables, traits of R_0 less than *1* and r greater than 0 result in a mean population increase (Southwood & Henderson, 2000; Chen *et al*., 2017). Our data support this theory, because they indicated that the semi-artificial diet was more suitable for the *B. dorsalis* due to higher fecundity and shorter development time than those of other three *Bactrocera* species.

In our study, we only compared the fitness of four *Bactrocera* flies by using two-sex life table on semi-artificial diet, which would be more useful for mass rearing of these flies. This study will be more helpful for future works, whether there are significant differences in fitness parameters of fruit flies on this semi-artificial diet and natural host. We suggest that our study will be helpful in the mass rearing, study of molecular biology, and sterile insect techniques for *Bactrocera* species, especially for *B. dorsalis*, *B. correcta*, *B. cucurbitae* and *B. tau*. In addition, based on the results of life table study, we could better understand when (and why) the populations of *Bactrocera* species suffer high mortality. In this way, a plan for the IPM of *Bactrocera* species would be timely conducted.

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References

Allwood, A., Chinajariyawong, A., Kritsaneepaiboon, S., Drew, R., Hamacek, E., Hancock, D., Hengsawad, C., Jipanin, J., Jirasurat, M. & Krong, C.K. (1999) Host plant records for

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fruit flies (Diptera: Tephritidae) in Southeast Asia. *Raffles Bulletin of Zoology* **47**, 1–92.

Awmack, C.S. & Leather, S.R. (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* **47**, 817–844.

Birch, L.C. (1948) The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology* **17**, 15–26.

Castañé, C. & Zapata, R. (2005) Rearing the predatory bug *Macrolophus caliginosus* on a meat-based diet. *Biological Control* **34**, 66–72.

Chang, C.L., Caceres, C. & Jang, E.B. (2004) A novel liquid larval diet and its rearing system for melon fly, *Bactrocera cucurbitae* (Diptera: Tephritidae). *Annals of the Entomological Society of America* **97**, 524–528.

Changmu, J. & Hongmu, A. (2006) Life tables of the melon fly laboratory population reared on various host fruits. *Journal of Fujian Agriculture and Forestry University* **35**, 24–28.

Chen, Q., Li, N., Wang, X., Ma, L., Huang, J.B. & Huang, G.H. (2017) Age-stage, two-sex life table of *Parapoynx crisonalis* (Lepidoptera: Pyralidae) at different temperatures. *PLoS ONE* **12**, e0173380.

Chi, H. & Su, H.Y. (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.

Chi, H. & Team C. (2017) *TWOSEX-MSChart: A Computer Program for the Age-Stage, Two-sex Life Table Analysis*. National Chung Hsing University, Taichung, Taiwan.

Clarke, A.R., Armstrong, K.F., Carmichael, A.E., Milne, J.R., Raghu, S., Roderick, G.K. & Yeates, D.K. (2005) Invasive phytophagous pests arising through a recent tropical evolutionary radiation: the *Bactrocera dorsalis* complex of fruit flies. *Annual Review of Entomology* **50**, 293–319.

Dhillon, M., Singh, R., Naresh, J. & Sharma, H. (2005) The melon fruit fly, *Bactrocera cucurbitae*: a review of its biology and management. *Journal of Insect Science* **5**, 40.

Dominiak, B.C., Sundaralingam, S., Jiang, L., Jessup, A.J. & Barchia, I.M. (2010) Impact of marker dye on adult eclosion and flight ability of mass produced Queensland fruit fly *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). *Australian Journal of Entomology* **49**, 166–169.

Drew, R.A.I. (2004) Biogeography and speciation in the *Dacini* (Diptera: Tephritidae: Dacinae). *Bishop Museum Bulletin in Entomology* **12**, 165–178.

Drew, R. & Raghu, S. (2002) The fruit fly fauna (Diptera: Tephritidae: Dacinae) of the rainforest habitat of the Western Ghats, India. *Raffles Bulletin of Zoology* **50**, 327–352.

Ekesi, S., Nderitu, P.W. & Chang, C.L. (2007) Adaptation to and small-scale rearing of invasive fruit fly *Bactrocera invadens* (Diptera: Tephritidae) on artificial diet. *Annals of the Entomological Society of America* **100**, 562–567.

Ekesi, S., De Meyer, M., Mohamed, S.A., Virgilio, M. & Borgemeister, C. (2016) Taxonomy, ecology, and management of native and exotic fruit fly species in Africa. *Annual Review of Entomology* **61**, 219–238.

Goodman, D. (1982) Optimal life histories, optimal notation, and the value of reproductive value. *The American Naturalist* **119**, 803–823.

Gupta, J. & Verma, A. (1978) Screening of different cucurbit crops for the attack of the melon fruit fly, *Dacus cucurbitae* Coq. (Diptera: Tephritidae). *Haryana Journal of Horticultural Sciences* **7**, 78–82.

Hasyim, A., Muryati, M. & De Kogel, W. (2016) Population fluctuation of adult males of the fruit fly, *Bactrocera tau* Walker (Diptera: Tephritidae) in passion fruit orchards in relation to abiotic factors and sanitation. *Indonesian Journal of Agricultural Science* **9**, 29–33.

Huang, Y.B. & Chi, H. (2012) 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**, 263–273.

Huang, Y.B. & Chi, H. (2013) Life tables of *Bactrocera cucurbitae* (Diptera: Tephritidae): with an invalidation of the jackknife technique. *Journal of Applied Entomology* **137**, 327–339.

Jiang, F., Li, Z.H., Deng, Y.L., Wu, J.J., Liu, R.S. & Buahom, N. (2013) Rapid diagnosis of the economically important fruit fly, *Bactrocera correcta* (Diptera: Tephritidae) based on a species-specific barcoding cytochrome oxidase I marker. *Bulletin of Entomological Research* **103**, 363–371.

Jiang, H.B., Gui, S.H., Xu, L., Pei, Y.X., Smagghe, G. & Wang, J.J. (2017) The short neuropeptide F modulates olfactory sensitivity of *Bactrocera dorsalis* upon starvation. *Journal of Insect Physiology* **99**, 78–85.

Katsoyannos, B., Boller, E. & Remund, U. (1977) Beitrag zur entwicklung von methoden fur die massenzucht der kirschenfliege, *Rhagoletis cerasi* L., auf kunstlichen substraten. *Mitteilungen Schweizerischen Entomologischen Gesellschaft* **50**, 25–33.

Kogan, M., & Bajwa, W.I. (1999) Integrated pest management: a global reality? *Anais da Sociedade Entomológica do Brasil* **28**, 01–25.

Kushwaha, K., Pareek, B. & Noor, A. (1973) Fruit fly damage in cucurbits at Udaipur. *Udaipur University Research Journal* **11**, 22–23.

Lall, B. & Sinha, S. (1959) On the biology of the melon fly, *Dacus cucurbitae* (Coq.) (Diptera: Tephritidae). *Science & Culture* **25**, 159–161.

Leslie, P.H. (1945) On the use of matrices in certain population mathematics. *Biometrika* **33**, 183–212.

Lewis, E.G. (1977) On the generation and growth of a population. pp. 221–225 in *Mathematical Demography*. Biomathematics, vol 6. Springer, Berlin, Heidelberg.

Liu, J.L., Chen, X.Y. & Zeng, X.N. (2015) Classical olfactory conditioning in the oriental fruit fly, *Bactrocera dorsalis*. *PLoS ONE* **10**, e0122155.

Liu, X., Jin, Y. & Ye, H. (2013) Recent spread and climatic ecological niche of the invasive guava fruit fly, *Bactrocera correcta*, in mainland China. *Journal of Pest Science* **86**, 449–458.

Mir, S., Dar, S., Mir, G. & Ahmad, S. (2014) Biology of *Bactrocera cucurbitae* (Diptera: Tephritidae) on cucumber. *Florida Entomologist* **97**, 753–758.

Mittler, T. & Tsitsipis, J. (1973) Economical rearing of larvae of the olive fruit fly, *Dacus oleae*, on a liquid diet offered on cotton towelling. *Entomologia Experimentalis et Applicata* **16**, 292–293.

Pozuelo, M., Chang, Y., & Yang, J. (2015) Effect of diamondoids on the microstructure and mechanical behavior of nanostructured Mg-matrix nanocomposites. *Materials Science and Engineering: A* **633**, 200–208.

Rabab, R.A., Al-Eryan, M., El-Minshawy, A. & Gadelhak, G. (2016) Laboratory rearing of the peach fruit fly *Bactrocera zonata* (Saunders) (Diptera: Tephritidae) on semi-artificial diet based on soybean protein. *Alexandria Journal of Agricultural Science* **61**, 175–183.

Rajaganapathi, J. & Kathiresan, K. (2002) A simple and cost-effective mass rearing technique for the tephritid fruit fly, *Bactrocera dorsalis* (Hendel). *Current Science* **82**, 266–268.

Razmjou, J. & Golizadeh, A. (2010) Performance of corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (Homoptera: Aphididae) on selected maize hybrids under laboratory conditions. *Applied Entomology and Zoology* **45**, 267–274.

SAS Institute (2009) SAS/STAT user's guide, version 9.2. SAS Institute, Cary, NC, USA.

Sayyed, A.H., Saeed, S. & Crickmore, N. (2008) Genetic, biochemical, and physiological characterization of spinosad resistance in *Plutella xylostella* (Lepidoptera: Plutellidae). *Journal of Economic Entomology* **101**, 1658–1666.

Shen, K., Hu, J., Wu, B., An, K., Zhang, J., Liu, J. & Zhang, R. (2014) Competitive interactions between immature stages of *Bactrocera cucurbitae* (Coquillett) and *Bactrocera tau* (walker) (Diptera: Tephritidae) under laboratory conditions. *Neotropical Entomology* **43**, 335–343.

Shinwari, I., Khan, S., Khan, M.A., Ahmad, S., Shah, S.F., Mashwani, M.A. & Khan, M.A. (2015) Evaluation of artificial larval diets for rearing of fruit fly *Bactrocera zonata* (Diptera: Tephritidae) under laboratory condition. *Journal of Entomology and Zoology Studies* **3**, 189–193.

Singh, P. (1977) *Artificial Diets for Insects, Mites and Spiders*. IFI/Plenum Publishing Company, New York, USA.

Singh, S.K., Kumar, D. & Ramamurthy, V.V. (2010) Biology of *Bactrocera* (*Zeugodacus*) *tau* (walker) (Diptera: Tephritidae). *Entomological Research* **40**, 259–263.

Southwood, T. & Henderson, P. (2000) *Ecological Methods*. Oxford, Blackwell Science Ltd.

Tan, K.H., Tokushima, I., Ono, H. & Nishida, R. (2011) Comparison of phenylpropanoid volatiles in male rectal pheromone gland after methyl eugenol consumption, and molecular phylogenetic relationship of four global pest fruit fly species: *Bactrocera invadens*, *B. dorsalis*, *B. correcta* and *B. zonata*. *Chemoecology* **21**, 25–33.

Vargas, R.I. & Carey, J.R. (1989) Comparison of demographic parameters for wild and laboratory-adapted Mediterranean fruit fly (Diptera: Tephritidae). *Annals of the Entomological Society of America* **82**, 55–59.

Vargas, R.I., Walsh, W.A., Kanehisa, D., Jang, E.B. & Armstrong, J.W. (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., Walsh, W.A., Kanehisa, D., Stark, J.D. & Nishida, T. (2000) Comparative demography of three Hawaiian fruit flies (Diptera: Tephritidae) at alternating temperatures. *Annals of the Entomological Society of America* **93**, 75–81.

Varley, G. & Gradwell, G. (1970) Recent advances in insect population dynamics. *Annual Review of Entomology* **15**, 1–24.

Vayssières, J.F., Carel, Y., Coubes, M. & Duyck, P.F. (2008) Development of immature stages and comparative demography of two cucurbit-attacking fruit flies in Reunion Island: *Bactrocera cucurbitae* and *Dacus ciliatus* (Diptera Tephritidae). *Environmental Entomology* **37**, 307–314.

Waseem, M., Naganagoud, A., Sagar, D. & Kareem, M.A. (2012) Biology of melon fly, *Bactrocera cucurbitae* (Coquillett) on cucumber. *BIOINFOLET-A Quarterly Journal of Life Sciences* **9**, 232–239.

White, I.M. & Elson-Harris, M.M. (1992) *Fruit Flies of Economic Significance: Their Identification and Bionomics*. Wallingford, CAB International.

Yang, P., Carey, J. & Dowell, R. (1994) Host-specific demographic studies of wild *Bactrocera tau* (walker) (Diptera: Tephritidae). *The Pan-Pacific Entomologist* **70**, 253–258.